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ANATOMICAL AND PHYSIOLOGICAL STUDIES ON THE GROWTH OF THE INNER EAR OF THE ALBINO RAT

TOKUJIRO WADA
THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY

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MEMOIRS

OF

THE WISTAR INSTITUTE OF ANATOMY AND BIOLOGY

No. 10

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TOKUJIRO WADA

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ANATOMICAL AND PHYSIOLOGICAL STUDIES ON THE GROWTH OF THE INNER EAR OF THE ALBINO RAT

INTRODUCTION

Since Alphonse Corti, in 1851, published his famous work on the cochlea of mammals, studies on this organ have been made by many authors and have produced fairly concordant results. Concerning the postnatal growth of the internal ear, however, systematic studies are lacking. Especially is there no investigation, so far as I know, on the growth of the nerve cells in the ganglion spiral, not even in the great work of Retzius. ('84).

It was the special object of these studies, therefore, to follow the growth of the cells forming the spiral ganglion from birth to maturity and to correlate the changes in them with the appearance of the functional responses and with the structural changes in the membranous cochlea. In the course of this investigation studies were made also on the cells of the ganglion vestibulare, in order to see whether these cells differed in their growth from the cells in the spiral ganglion. Both of these ganglia are situated in the course of nervus acusticus, but have, as is well known, entirely different functions.

Thus determinations have been made on the diameters of the cells of the ganglion spirale and of their nuclei at different ages; of the nucleus-plasma ratios and of their growth in relation to those of other portions of the membranous cochlea. For the cells of the vestibular ganglion similar determinations were also made. Finally, these results have been compared with those obtained from the study of other craniospinal ganglia in the albino rat.

In presenting my results I shall begin with a description of the changes in the larger portions of the membranous cochlea and pass from these to the cell elements themselves, and then to the observations on the ganglion cells and to the correlation between hearing and the growth of the cochlea.

MATERIAL

For the present studies forty male and thirty female albino rats were used, representing every phase of postnatal growth and having approximately standard body weights. These were all from the colony of The Wistar Institute, and were sometimes from the same, and sometimes from different litters.

At first all these rats were tested for their ability to hear and their equilibrium, and it was ascertained that after about twelve days of age, or somewhat earlier, they responded positively to the test for hearing. Such examinations were deemed necessary, to make certain that the rats used were normal.

I have arranged the animals thus tested in fourteen groups according to age, each group having five individuals in it. Serial sections from all these cochleas were made by methods to be given later. Most of them were in the plane of the vertical axis of the cochlea, but some were at right angles to it.

From the former I selected four ears in each group for the study of the growth of the cochlea. For the study of the growth of the ganglion vestibulare, I have used for the most part the same specimens. For the study of the sections at right angles to the vertical axis of the cochlea, sections from one ear of each group were used.

TECHNIQUE

In order to obtain good preparations of this delicate organ, the method of vital fixation (injection under anaesthesia) was used. The method employed, and which proved almost ideal, was that introduced by Metzner and Yoshii ('09), Siebenmann and Yoshii ('08) and somewhat improved by Sato ('17). After the animals had been tested to make sure that they were quite normal, the fixing solution was injected through the aorta under ether. The brain was then carefully removed, care being taken not to drag the trunk of the nervus acusticus, as noted by Nager ('05), and the bulla tympanica was opened to allow the further penetration of the fluid.

The bony labyrinth with its surrounding bones was then placed in the fixing solution for two weeks, the fluid being renewed every day.

The fixing solution which I used consists, according to Yoshii ('09), of—

10 per cent formol	74 parts
Müller's fluid	24 parts
Glacial acetic acid	2 parts

According to Tadokoro and Watanabe ('20), this solution is one of the best, ranking with that of Wittmaack ('04, '06) and that of Nakamura ('14).

This injection method is sometimes difficult to apply to very young rats on account of the small size and the delicacy of the vessels. When injection failed in very young animals, then immediately the head was cut off and put directly in the fixing fluid. Owing to the incomplete calcification of the very young cochlea, the fixing solution enters rapidly and fixes the deep-seated organs in good condition. Since the parts of the internal ear are not yet well developed in the very young rats, they do not suffer from this method of fixation as do the older cochleas.

Indeed, no differences are to be seen between the sections prepared by vital fixation and by decapitation in very young rats.

For decalcification I have employed the following solution during three days, renewing it every day.

Decalcifying fluid

5 per cent aqueous nitric acid	49 parts
10 per cent formol	49 parts
Glacial acetic acid	2 parts

After the specimens had been washed in running water for three days, they were passed through the alcohols from 50 to 97 per cent. For the imbedding I have used 'parlodion' with good results. Here it is to be mentioned that all the cochleas were treated in the same way, even unossified cochlea being passed through the decalcifying fluid, so that there should be absolutely no differences in treatment.

The next important matter is the determination of the plane of the section. For the measurement of growth changes it was necessary to obtain corresponding sections from the several cochleas. In an organ like that of Corti, which changes in its details from one end to the other, however, it is very difficult to accomplish this, but I believe that I have overcome most of the difficulties.

After much testing, I found that a section parallel to the under surface of os occipitale in the fronto-occipital direction runs nearly exactly parallel to the axis of the modiolus of the cochlea. In order to get the same direction from right to left, I have taken as the standard the transverse plane of the under surface of the os occipitale, controlling the direction of the section with a magnifying glass. Thus nearly the same radial direction and nearly corresponding places in the cochlea were obtained in the several series of sections. This makes possible a trustworthy comparison of the measurements and drawings.

The cross-section of the cochlea was gotten by making the plane of the cut transverse to the axis of the modiolus. To get the corresponding levels is difficult. At first I divided all the serial sections by $2\frac{1}{2}$, which is the number of complete turns in the cochlea of the albino rat. Next, from the number of the slides representing each turn, I determined nearly the corresponding level in the cochlea according to age.

All the sections were 10μ in thickness. The sections were stained for the most part with haematoxylin and eosin, but sometimes by Heidenhain's iron haematoxylin or the iron haematoxylin and Van Gieson's stain. For the measurements, however, only the sections stained with haematoxylin and eosin were used.

For the examination of the larger parts of the cochlea and their relations, the sections were projected on a sheet of paper by the Leitz-Edinger projection apparatus, at a magnification of exactly a hundred diameters, and the outline of the image accurately traced. The remaining measurements of the ganglion cells and the smaller portions of the cochlea were made directly under the microscope. The measurements made on the tympanic

wall of the cochlea are somewhat complicated, but by the aid of figures 1 and 2 they may be explained. In figure 1 lines 1–1, 1–1′. 2–2, 3–3 indicate, respectively, the height of the arch of Corti, of the tunnel of Corti, of the papilla spiralis (Huschke) at the third series of outer hair cells, and of Hensen's supporting cells, respectively, above the plane of the membrana basilaris.

Lines 4–4′ which are the extensions of the surface of the lamina reticularis and of the membrana basilaris, subtend the angle θ.

To get the exact measurements of the radial breadth of the membrana tectoria is very difficult, if not impossible, because it is sinuous in its course; moreover, it differs in thickness from point to point. Therefore, it has been variously described by different authors. Intra vitam fixation tends to prevent distortion. We divide the membrana tectoria, figure 1, into two portions, the first or inner (7–7′–9–9′) and the second or outer (5–5′–7–7′) or outer zones of Retzius; each of these is again divided in two at 6–6′ and 8–8′, as shown in figure 1.

I have measured the radial distance of each portion and added all four together. This total approximates the natural radial breadth of this membrane, and since the sections have all been prepared in the same way and examined by the same method, the relations during growth can be followed.

In figure 2, 1–1 and 2–2, mark the length of the inner and outer pillar cells, respectively, from base to the point, which is situated just under their junction. It is to be noted here that the term 'pillar cell' here applies to the pillars in the strict sense and does not include the associated cells.

Distances 3 and 7 in figure 2 show the basal breadth of the inner and outer pillars, respectively. The former is identical with the distance between the habenula perforata and the outer corner of the inner pillar after the inner corner of the pillar has reached the habenula perforata, but there is some difference between the two distances in very young rats. Distance 4 is that between the habenula perforata and the inner corner of the outer pillar; distance 5 is that between the habenula perforata and the outer corner of the outer pillar. The latter represents at the same time the radial breadth of the zona arcuata of the membrana basilaris.

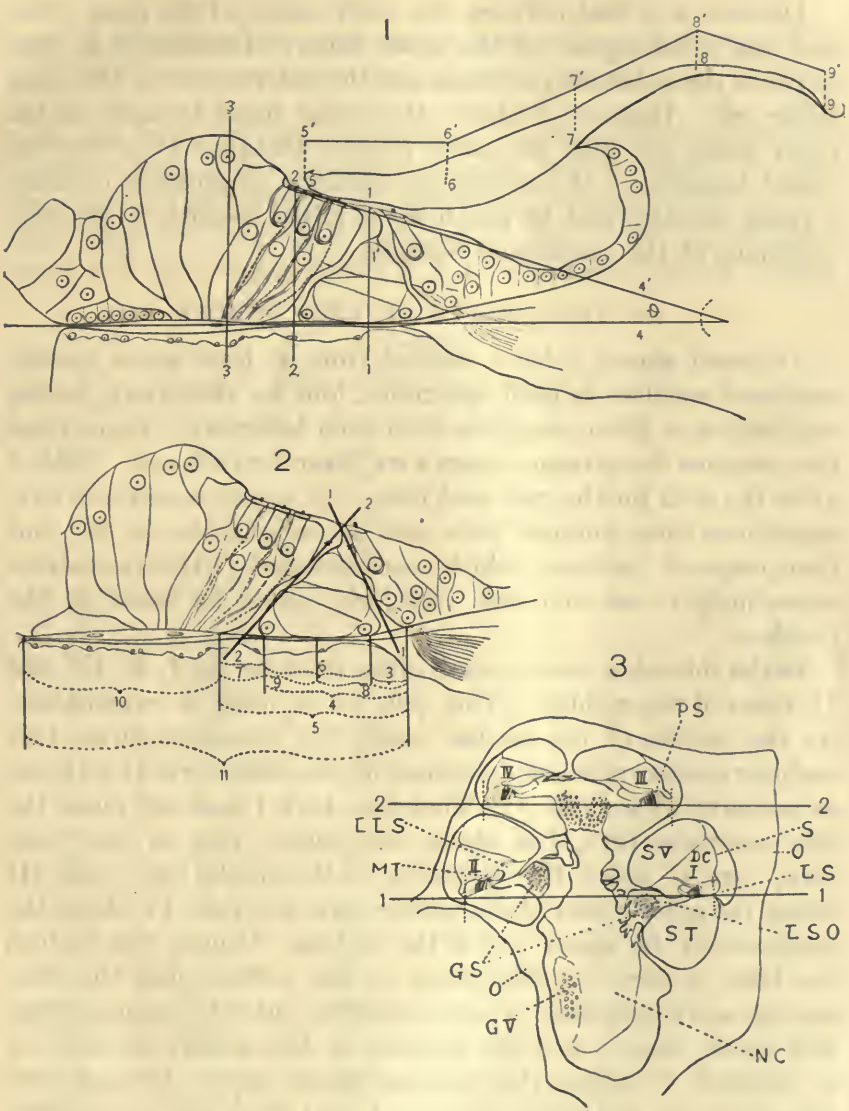
Fig. 1 Showing the localities for the measurement of each part of the tympanic wall of ductus cochlearis in the albino rat, 100 days old—radial vertical section. *1–1*, height from the basal plane to the surface of pillar cells; *1–1′*, greatest height of the tunnel of Corti; *2–2*, height of papilla spiralis at the third series of the outer hair cells; *3–3*, height of Hensen's supporting cells; *4–4′*, *4* indicates the extension of the membrana basilaris and *4′* the extension of the lamina reticularis. The two lines subtend the angle θ. The radial breadth of the membrana tectoria is taken as the sum of the four segments between the lines *5–5′* and *9–9′*.

Fig. 2 Showing the method of measurement for several parts of the tympanic wall of the ductus cochlearis in the albino rat, 100 days old. *1–1*, length of inner pillar cell without head; *2–2*, length of outer pillar cell without head Distance 3 shows radial distance between habenula perforata and the outer corner of inner pillar at base—after twelve days of age this equals the radial basal breadth of inner pillar. Distance 4, radial distance between habenula perforata and the inner corner of outer pillar at base. Distance 5, radial breadth of the zona arcuata (Deiters') of membrana basilaris, and at the same time it indicates radial distance between habenula perforata and the outer corner of outer pillar at base. Distance 6, radial distance between the outer corner of inner pillar and the inner corner of outer pillar at base. Distance 7, radial basal breadth of outer pillar. Distance 8, radial distance between the habenula perforata and outer corner of inner pillar cell at base. Distance 9, radial basal breadth of the outer pillar cell. Distance 10, radial breadth of zona pectinata of the membrana basilaris. Distance 11, radial breadth of entire membrana basilaris.

Fig. 3 Showing the general outline of the cochlea in the radial vertical section—albino rat, 100 days of age.

ABBREVIATIONS

Line *1*, *1*, distance between two basal spiral ligaments
Line *2*, *2*, distance between two apical spiral ligaments
I, first turn
II, second turn
III, third turn
IV, fourth turn
D.C., ductus cochlearis
G.S., ganglion spirale
G.V., ganglion vestibulare
L.L.S., limbus laminae spiralis
L.S., ligamentum spirale
L.S.O., lamina spiralis ossea
M.T., membrana tectoria
N.C., nervus cochlearis
O., bone
P.S., papilla spiralis
S., stria vascularis
S.T., scala tympani
S.V., scala vestibuli


1
2
3
PS
SV
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I
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S
O
LS
LSO
GS
GV
NC
MT
LLS

Distance 6 is that between the outer corner of the inner pillar and the inner corner of the outer pillar. Distance 8 is that between the habenula perforata and the outer corner of the inner pillar cell. Distance 9 shows the radial basal breadth of the outer pillar cell plus the outer pillar. Distance 11 shows the radial breadth of the membrane basilaris comprising distance 5 (zona arcuata) and 10, which is the radial breadth of the zona pectinata of the membrana basilaris.

ON THE GROWTH OF THE COCHLEA

As noted above, I have selected from at least seven serially sectioned cochleas in each age group, four for this study, taking one section in good condition from each labyrinth. From these four sections the average values were taken for each age. Table 1 gives the data for the rats used here. As we see, sometimes two, sometimes three animals were used at each age to get the four best-prepared sections which corresponded. Determinations accordingly to sex and side, therefore, cannot be based on like numbers.

In the following text we shall often refer to the I, II, III and IV turns of the cochlea. This calls for a word of explanation. As the cochlea of the rat has nearly 2½ complete turns, four cochlear canals are usually obtained in the radial vertical sections, as prepared by me (fig. 3). Therefore, turn I does not mean the first complete turn, but about the middle part of the basal turn; turn II about the beginning of the middle turn; turn III about the middle part of the middle turn, and turn IV about the beginning of the apical turn of the cochlea. Usually the cochlea has been divided for description by the authors into the first, second, and third turns, or more definitely into the basal, middle, and apical turns. For the purpose of this study, however, it is desirable to adopt the divisions given above, because here measurements are largely employed, and there are some differences in size, volume, and arrangement of structures, even between the beginning and end of the same turn.

At all events, it is to be kept in mind that such divisions are arbitrary, as the changes in the elements take place in a graded manner.

A. On the growth of the radial distance between the two spiral ligaments (fig. 3, 1–1, 2–2)

As we have usually four sections of the ductus cochlearis, therefore four spiral ligaments in one radial vertical section, there are two radial distances presented, the first, figure 3, 1–1, connecting the two basal sections of the ductus on opposite sides, and the second, figure 3, 2–2, connecting the two apical

TABLE 1

Data on the albino rats used for the study of the cochlea

AGE	BODY WEIGHT	BODY LENGTH	SEX	SIDE	HEARING
days	*grams*	*mm.*			
1	5.3	48	♂	R. L.	—
1	4.2	47	♂	R. L.	—
3	8.8	60	♂	R.	—
3	7.1	54	♂	R. L.	—
3	8.2	56	♀	R.	—
6	10.2	64	♀	R. L.	—
6	11.0	62	♂	R. L.	—
9	9.1	58	♀	R. L.	—
9	9.8	57	♂	R. L.	±
12	13.0	70	♂	L.	+
12	11.9	68	♀	R. L.	+
12	14.8	72	♂	L.	+
15	13.0	74	♂	R.	+
15	13.5	75	♀	R.	+
15	13.0	74	♀	R. L.	+
20	30.0	96	♂	R. L.	+
20	28.0	94	♂	R. L.	+
25	38.4	107	♀	R. L.	+
25	34.2	101	♀	R. L.	+
50	60.0	128	♀	R. L.	+
50	57.5	121	♀	R. L.	+
100	145.6	176	♂	L.	+
100	102.5	154	♀	R.	+
100	100.5	152	♀	R. L.	+
150	153.5	184	♀	R.	+
150	188.9	191	♂	R. L.	+
150	198.8	192	♂	R.	+
250	133.5	178	♀	R. L.	+
263	140.3	171	♀	R. L.	+
365	205.4	202	♂	L.	+
365	170.4	182	♀	R. L.	+
368	179.0	196	♀	R.	+
546	282.1	222	♂	R. L.	+
546	227.1	204	♂	R. L.	+

sections. These distances measure the radial breadth of the membranous cochlea and of the modiolus combined at these levels.

In table 2 (chart 1) are entered the values for the radial distances found between the two spiral ligaments in fourteen

TABLE 2

Radial distance between the two spiral ligaments in radial-vertical section (chart 1, figure 3)

AGE	BODY WEIGHT	AVERAGE DISTANCE BETWEEN TURNS IN μ		
		I–II	III–IV	I–II plus III–IV
days	*grams*			*mean*
1	5	1410	925	1168
3	8	1560	1025	1293
6	11	1650	1175	1413
9	10	1635	1225	1430
12	13	1640	1233	1437
15	13	1655	1235	1445
20	29	1645	1250	1448
25	36	1620	1250	1435
50	59	1615	1253	1434
100	112	1663	1270	1467
150	183	1618	1290	1454
257	137	1655	1275	1465
366	181	1635	1285	1460
546	255	1680	1265	1473

Ratios 1 — 12 days 1 : 1.2
1 — 20 " : 1.2
1 — 546 " : 1.3

TABLE 3—*Condensed*

Ratios of distances between the two spiral ligaments along 1–1 (turns I–II) and along 2–2 (turns III–IV), figure 3

AGE	BODY WEIGHT	Ratios between the two distances—turns I–II and III–IV
days	*grams*	
1	5	1 : 0.66
8	11	: 0.72
18	21	: 0.75
213	138	: 0.77

age groups, from one to 546 days. As we see, the average value of the two distances grows rapidly from birth till six days of age. After that period the value increases gradually till twenty days, while after twenty days the increase is very slight indeed. The ratios between 1 and 12, 1 and 20, and 1 and 546 days show these relations.

In table 3 are given the average ratios between two radial distances between I–II and III–IV at four ages. Here we can also see a rapid increase in the ratio from one to eight days of age, while afterwards the ratios rise very gradually. The data in table 2 show that at nine days the mean diameter of the bony cochlea as thus measured is approximately 97 per cent of the value at maturity. The cochlea thus attains nearly its full size at an early age. Chart 1 illustrates this point.

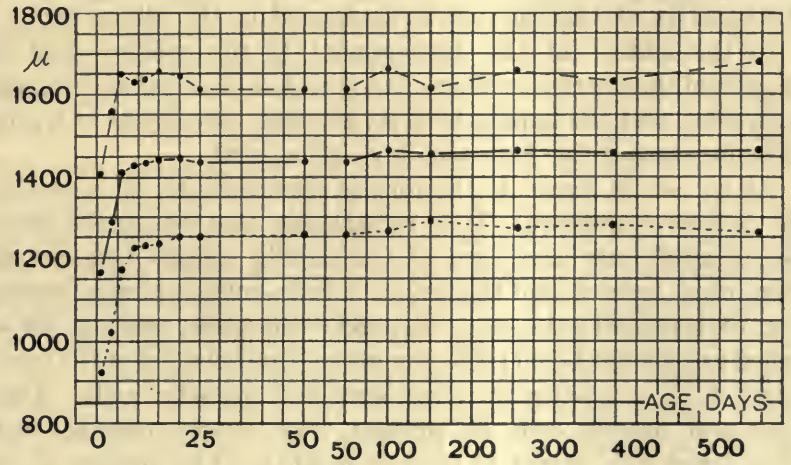


Chart 1 The radial distance between the spiral ligaments, turns I–II and III–IV, table 2, figure 3 (*1–1*) and (*2–2*).

———— Radial distance at turns I–II.

..... Radial distance at turns III–IV.

———— Average radial distance for the two foregoing measurements.

All the charts are plotted on age.

The scale for age changes at 50 days. From 0 to 50 days one interval is equal to five days. From 50 days on, one interval is equal to twenty-five days.

Unless otherwise stated, the measurements recorded in these charts have been made on radial-vertical sections.

B. On the growth of the tympanic wall of the ductus cochlearis

Figures 4 to 12 show the appearance in outline at birth, at three six, nine (not hearing), nine (hearing), twelve, twenty one hundred, and 546 days, respectively. These figures have been drawn from the best corresponding sections at the beginning of the middle turn of the cochlea, figure 3, turn II, which I have selected as the type, as did Retzius.

The fact, demonstrated by many authors, Böttcher ('69), Retzius ('84), and others, that development progresses from the basal to the apical turn is confirmed in the albino rat.

In the albino rat the development of the cochlea, and especially of the ductus cochlearis, is somewhat retarded as compared with man, and the papilla with its elements developed in a great measure during the first ten days after birth.

As we see in figure 4, the ductus cochlearis in the new-born rat is very immature. It is remarkable that the space which lies in adult rats axialward of the papilla spiralis between the membrana tectoria and the limbus spiralis-sulcus spiralis internus (fig. 10) is not yet to be seen. Instead of the space, there is the so-called greater epithelial ridge (der grosse Epithelwulst of Böttcher) figure 4, G. consisting of pseudostratified epithelial cells. These long and narrow cells lie pressed very closely together with their large oval nuclei at various heights. The surface of the prominence sinks slightly in its center, and at the outer end of the prominence more rapidly, where it passes over into the so-called lesser epithelial ridge fig. 4, L. (der kleine Epithelwulst) at an obtuse angle.

The latter is, of course, a relatively small prominence, making up the greater part of the papilla spiralis. The pillar cells of Corti lie with their upper ends at the most inner part of the surface of the lesser ridge just in the angle with the greater ridge. They form two entirely separate rows of cells, the inner and the outer, but so close together that we cannot detect any space between them. Only the protoplasm of the inner pillar cell is more transparent above the nucleus, and on the inward side there is a thin rod passing from the upper end to the lower

part near the base. This transparent area is not the locus of the future tunnel of Corti, but marks the protoplasmic change into the pillar, as the transparent substance condenses into the rod. We can see this change beginning in the basal turn before it appears in the apical turn of the cochlea. The inner and outer cells make a triangle with a narrow base, which clings to the membranea basilaris; they turn somewhat outward.[1]

A large oval nucleus lies in the basal part of each cell; that of the inner pillar cell is very large, about twice as large as that of the outer, and with its long axis in a radial direction. As figure 4 shows, the inner corner of the inner pillar cell does not yet reach to the habenula perforata.

The hair cells, which in the albino rat are in four rows through all the turns, are separated by the pillar cells into two groups, the inner containing one and the outer three rows of cells. They are comparatively well developed at birth (fig. 4). The inner hair cell belongs to the greater ridge, as Kölliker ('67), Gottstein ('72), Retzius ('84), Held ('09), and others have already affirmed, and contrary to the assertaion of Böttcher ('69) and others.

It is situated in the most outer part of the declivity of the greater ridge and slants away from the axis with its round lower end at about half the height of the greater thickening. It has a large round nucleus in the base and the small hairlet at the top. This hair cell is nearly twice as large as the outer hair cells. The three outer hair cells reach down to the middle of the lesser ridge, not through it, having no process at their basal end. They end with their upper parts at the surface of the prominence. They stand not straight, but turn with their long axis very slightly inward, i.e., the in direction opposite to the long axis of the inner hair cells. They are cylindrical in form with a round nucleus at their base and small hairlet on the top.

Below the outer hair cells stand the three rows of Deiters' cells, which have large oval nuclei. These rest with their wide bases on the basilar membrane and their pointed ends reach to the surface of the epithelium. They are retarded in develop-

[1] In the following description of the cochlea, 'outward' means away from the axis 'inward' towards the axis.

ment, and at birth their cell bodies are short and undeveloped, so that they hardly suggest the adult cells.

Hensen's supporting cells (fig. 10, at maturity) are as yet undeveloped and nearly uniform in height, their nuclei being at nearly the same level.

Outward from the Hensen's cells the height of the epithelial cells at maturity rapidly diminishes and passes over to the cylindrical cells of sulcus spiralis externus. At birth no such distinction is present. Through all the turns the surface of the lesser epithelial ridge remains about parallel to the plane of the membrana basilaris.

The membrana basilaris, which stretches from the labium tympanicum outward to the crista basilaris of the ligamentum

Figs. 4 to 12 Showing the increase in size and morphological changes in each part of the tympanic wall of ductus cochlearis of the cochlea during growth, in the radial vertical section—albino rat. All the figures have been uniformly enlarged.

Fig. 4 One day. *G*, greater epithelial ridge; *L*, lesser epithelial ridge.

Fig. 5 Three days.

Fig. 6 Six days.

Figs. 7 to 8 Showing the differences in size and morphological changes in the tympanic wall of ductus cochlearis between a nine-day-old rat which can already hear (fig. 8) and one that cannot (fig. 7)

Fig. 9 Twelve days.

Fig. 10 Twenty days. In figure 10 we have drawn all the elements of the organ.

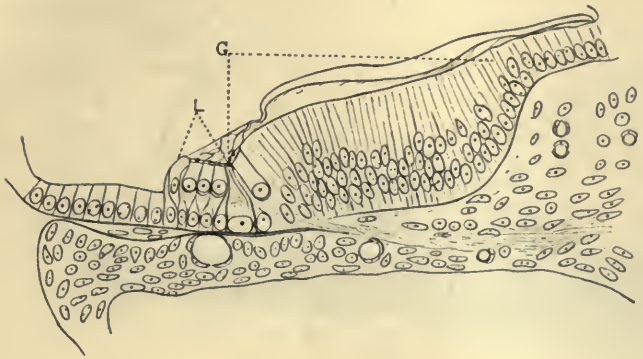
ABBREVIATIONS

M.T., membrana tectoria s. Corti
L.V., labium vestibulare of crista spiralis
S.S.I., sulcus spiralis internus
S.I.C., cells of sulcus spiralis internus
I.S., inner supporting cells
I.H., inner hair cells
O.H., outer hair cells
H.S.,Hensen's supporting cells
S.E.C., cells of sulcus spiralis externus
M.B.,membrana basilaris
I.P., inner pillar
O.P., outer pillar
B.C., basal cells
D.C., Deiters' cells
Bo.C., Boettcher's cells
L.S., ligamentum spirale
N.F., myelinated fibers of ramus acustici
R.F., radial fibers of ramus basilaris acustici in the tunnel of Corti
T., tunnel of Corti
B., blood vessels
O., bone

Fig. 11 One hundred days.

Fig. 12 546 days.

4



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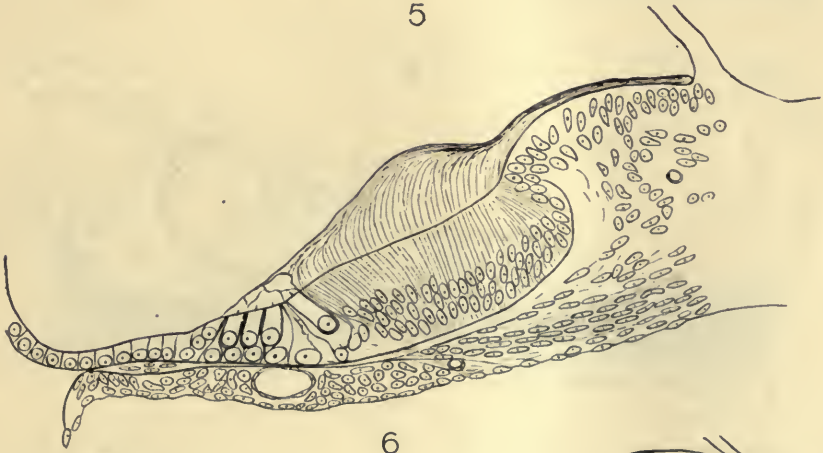

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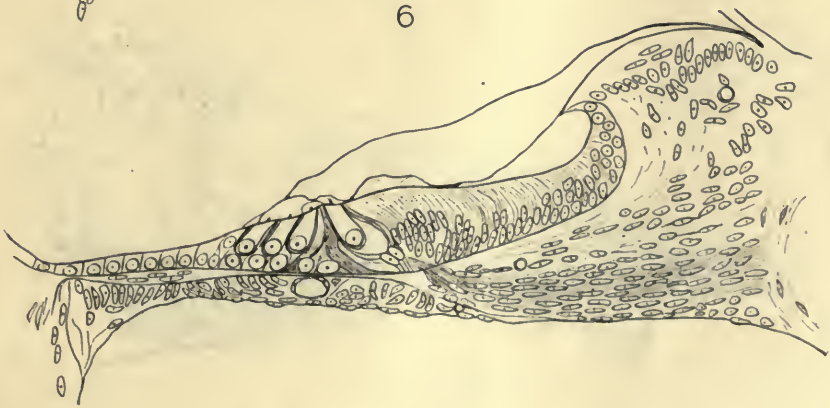

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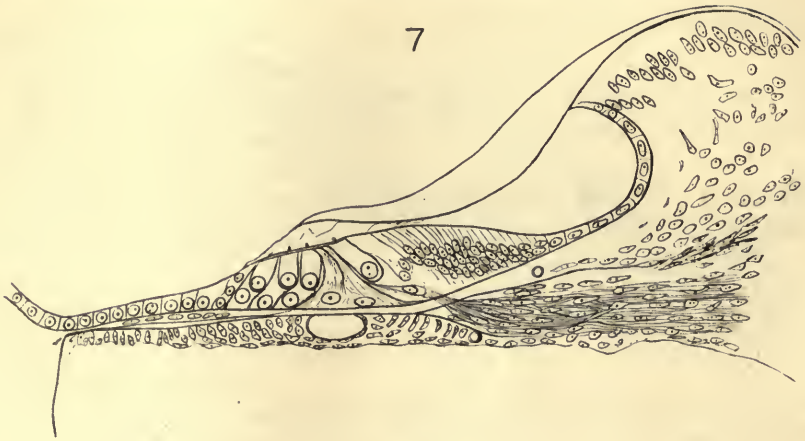

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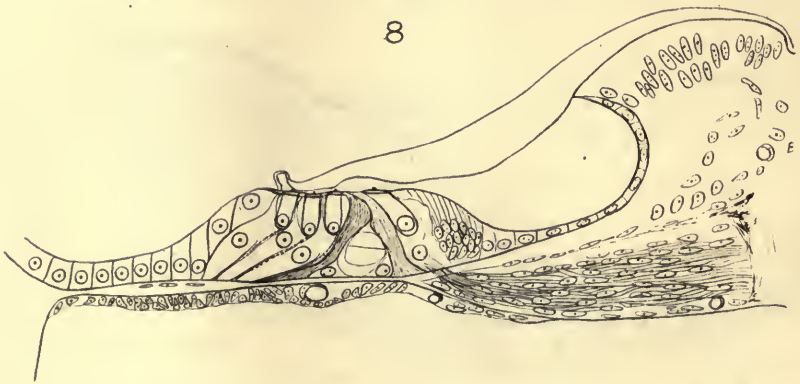

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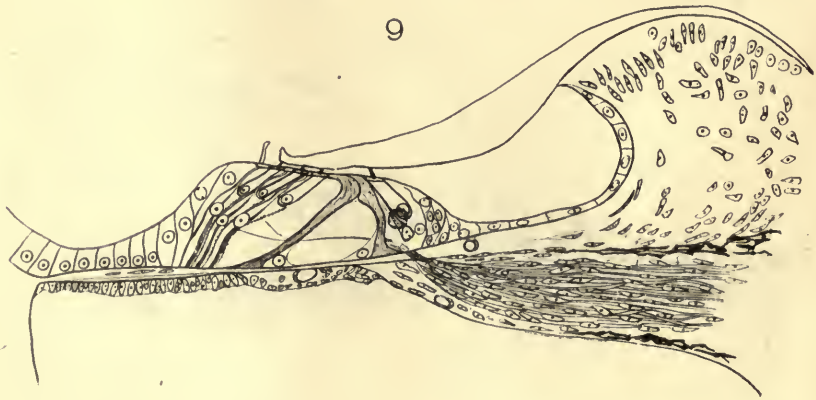

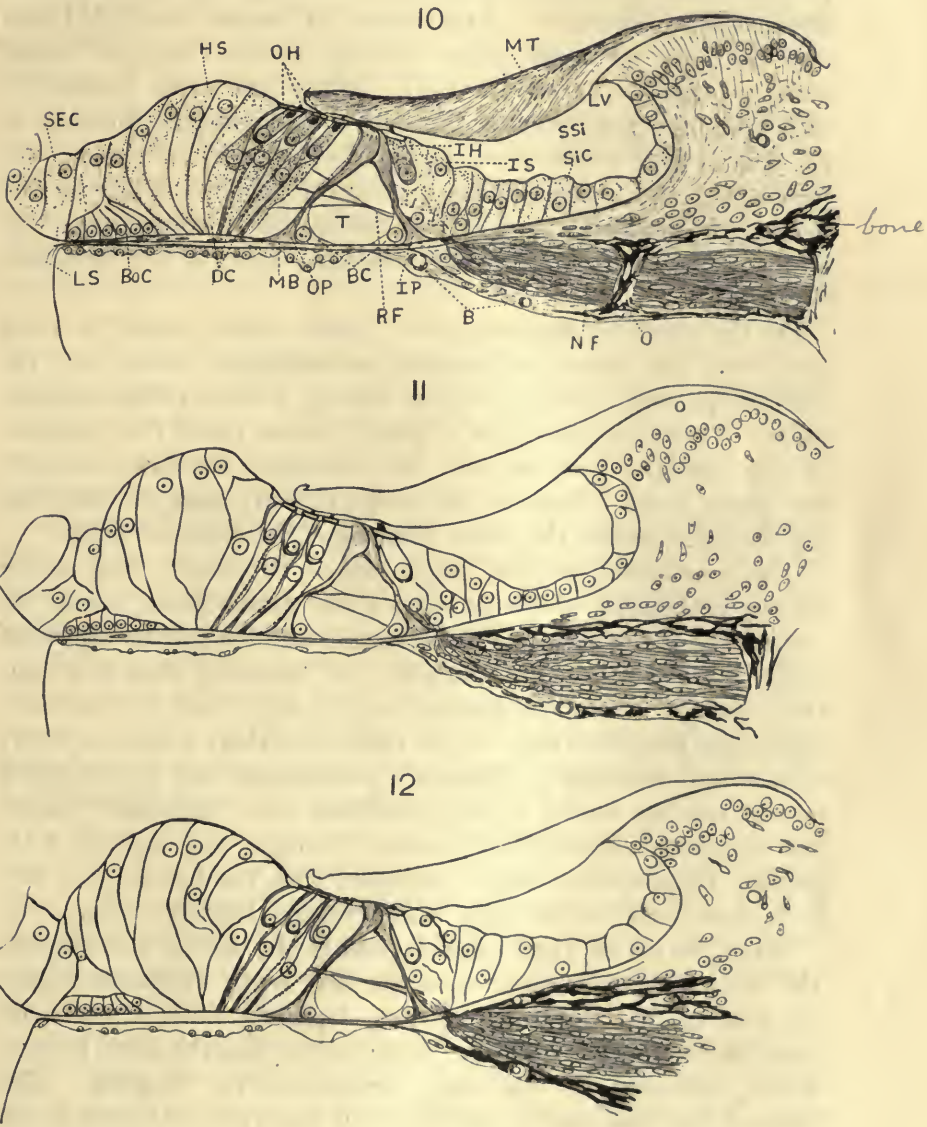
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spirale, consists of two layers, an upper, membrana basilaris propria, and an under, tympanic investing layer (tympanale Belegschicht: Retzius). The former, of course, is divided into two portions, an inner, zona arcuata (Deiters) and an outer, zona pectinata (Todd-Bowman). While the zona arcuata is thin from the beginning of life, the zona pectinata thickens at its central part where it contains cells with oblong nuclei. On passing to the spiral ligament it again becomes thin. In the young, the under layer is not so regular in structure as in the adult. The cells close to the basilaris propria are arranged vertically.

On the contrary the cells below them, which vanish in great part with age, have an irregular arrangement; those near the endothelial cells of scala tympani having a more radial arrangement. Therefore, this layer is thick, several times the thickness of the basilaris propria, and the thickness increases towards the upper turns. The vas spirale is strikingly large at this stage and lies just under the outer pillar and the Dieters' cells.

The membrana tectoria, beginning at the inner angle of the ductus cochlearis, where Reissner's membrane rises, covers the epithelium of the limbus laminae spiralis and the greater epithelial ridge, lying close to their surfaces. At the inner part it is thin, but thickens where the greater ridge begins, and at the outer part again becomes thin. In the basal turn there is seen as a very thin strand reaching to Hensen's prominence, but in the apical turn it reaches hardly to the inner hair cell. Although it gives rise to several thread-like processes going to the surface of the papilla, these do not seem to connect with the hairs of the hair cells, but with the terminal plates of the Dieters' cells.

When we divide the tympanic wall of the ductus cochlearis at the boundary between the greater and lesser epithelial ridges, we observe that the inner portion—from the inner angle to the outer end of the greater ridge—is far larger than the outer portion, which, however, is the more important for hearing. This relation becomes more evident as we pass from the base to the apex. Moreover, the total radial length of the tympanic wall

diminishes at this stage towards the apex, though it is larger in the beginning of the middle turn than in the middle of the basal turn. As will be shown later, these relations are entirely reversed in the adult cochlea. This fact indicates that the cochlea at this stage is very immature.

In the three-day-old rat the cochlea is much better developed (fig. 5). The radial breadth of the typmanic wall of the ductus cochlearis becomes greater in all the turns, especially in the upper turn; therefore the differences between the radial breadths in each successive turn are smaller than at the earlier stage. There is some change as we pass towards the apex in the relation of the inner and outer portion of the tympanic wall. At the basal turn and the beginning of the middle turn the radial breadth of the outer portion increases greatly, but diminishes again towards the apex. Although the radial breadth of the inner portion increases through all the turns, the proportion of this increase becomes greater towards the apex. As the inner portion is composed of the greater epithelial ridge and of the limbus laminae spiralis, and as the breadth of the latter diminishes towards the apex, the increase of the radial breadth of the inner portion is due to changes in the greater epithelial ridge.

The heights of the greater epithelial ridge, however, diminishes through the successive turns, becoming less and less from base to apex. Thus in the cochlea at this age it has a small radial breadth and vertical height in the basal turn and a larger radial breadth and height in the upper turns.

In all the turns the inner hair cell is inclined outwards and lies with its surface forming the outermost part of the greater ridge. The obtuse angle which it helps to make (fig. 5) as a boundary between the greater and lesser ridge in upper turns, vanishes in the basal turn where there is no sharp boundary between the two ridges.

The pillar cells of Corti develop more and more during this early stage; the radial breadth of their base increases, but as yet there is no space between them. They incline much more outwards than in the earlier stage. The protoplasmic change in the rod progresses, especially in the basal turn, and the head plate of the cell can be seen distinctly.

The outer hair cells become higher and wider; they are slightly inclined inward in the upper turn. On passing towards the basal turn the inclination inward increases, and in the basal turn it is most oblique, almost at 45°, to the plane of the basilar membrane. In figure 4 the inclination of these cells is only slight.

Deiters' and Hensen's cells are not well developed; the conditions are as in the former stage.

The plane of the surface of the lesser epithelial ridge is intimately related to the development of the outer hair cells and Deiters' cells, and as the latter are in an undeveloped condition, it runs nearly parallel to the plane of the membrana basilaris, sometimes dipping outward.

The membrana basilaris seems to be much longer; its composition is about the same as that in the one-day rat, only the thickness is somewhat decreased, owing to the reduction of the rows of cells in the tympanic layer.

The membrana tectoria grows in breadth and thickness, covering very closely the inner portion of the tympanic wall and connects outwards with Deiters' and Hensen's cells by slender fibrous processes—the so-called outer marginal zone. The hairs of the cells stand between these processes, but have no connection with them.

The vas spirale does not suffer reduction.

At six days (fig. 6) the development of the cochlea has proceeded futher. The radial breadth of the tympanic wall has increased. Thus we find the tympanic wall, especially its inner portion, increasing towards the apex, chiefly owing to the augmentation of the radial breadth of the greater ridge. In this a remarkable change is to be seen. In the basal turn the long slender cells disappear in the inner part of the greater ridge, and instead of them there are found cylindrical cells with oval nuclei near their bases.

The height of these cells increases gradually to the level of the surface of the inner hair cell; their upper surface is here in contact with the membrana tectoria. Thus a space appears between the cylindrical epithelium and the membrane—the sulcus

spiralis internus—which is deep and wide in the basal turn, becomes gradually shallow and narrow as we pass upward, and in the middle part of the middle turn is to be seen as a small and flat space. In the apical turn it is not yet present. The inner side of this space is made by the labium vestibulare of the limbus laminae spiralis.

As a result of this change in the greater ridge, the obtuse angle between the greater and lesser ridge vanishes entirely, and the two surfaces come to lie in the same place. The inner hair cell becomes larger and inclines less outward.

It is to be noted that the inner hair cell is supported on both sides by long slender cells. These have been variously described by several authors, but first Hans Held ('02) and afterwards Kolmer ('07) have considered them as supporting cells, reaching from the surface of the hair cell to the plane of the basilar membrane. Held has termed the cell which lies outward the 'Phalangenzelle.'

I have paid some attention to this cell and the changes in it. It is long and slender and stands between the inner hair cell and the inner pillar cell, with the upper end reaching to the surface, and is attached at its base to the inner corner of the inner pillar. The oblong oval nucleus lies in its basal portion. On the inner side of the inner hair cell there is a group of two to three cells of the same kind. These cells, termed 'Grenzzellen' by Held, stand near the habenula perforata, reach to the height of epithelium, and have their bases in intimate relation to the former.

These are not neuro-epithelial cells nor in intimate relation with the nerve fibers, but similar to the Deiters' cells which support the outer hair cells.

The developing pillar cells become progressively wider at their bases. The inner pillar cell sends a long foot towards the habenula perforata and in the basal turn it sometines reaches to it. The outer pillar cell increases its length very rapidly and extends its foot outward on the basilar membrane. Thus in the basal turn the triangle made by the inner and outer pillar cells and having a short base, in the upper turns changes to an equilateral

triangle and stands upright on the basilar membrane. In the apical turn the inner pillar cell is not yet so long as in the lower, turns and is still inclined outwards. The head plates and pillars are fairly prominent, but there is as yet no space between them.

The outer hair cells have grown and are inclined inward. Deiters' and Hensen's cells have not yet begun to develop, as have the other elements of the organ of Corti just described.

In the membrana basilaris we see the reduction of cells in the tympanic covering layer. The vas spirale shows more or less reduction. The membrana tectoria increases its radial breadth following the associated structures. The so-called marginal zone connects with Hensen's cells and the lamina reticularis by fibrous processes.

Among five nine-day-old rats, as shown later, one responded to the tests for hearing. As the majority of them gave no reaction, the cochlea of the latter, non-hearing rat, may be taken as the type for this age. The differences between the cochlea of the hearing and non-hearing rats will be mentioned later.

In rats of this age (fig. 7.) the cochlea is still further advanced. The sulcus spiralis internus appears through all the coils, and is deepest and broadest in the basal turn, diminishing in depth or gradually toward the apex. The cells covering the space are low and cuboid in the lower turns, but in the apical turn they are yet relatively high, cylindrical cells.

These cells probably have their origin from the long slender cells of the greater epithelial ridge, as Böttcher ('69) and others maintain, although Gottstein ('72) and some others think that they come by the outward migration of the epithelium of the limbus spiralis, and Retzius ('84) regards this latter view as the more probable.

The inner and outer hair cells become large and approach their mature form. The supporting cells of the inner hair cell are very evident.

The pillar cells develop more and more, their radial breadth increases and the pillars and headplates also become distinct. Sometimes we see a small space between the inner and outer pillar cells in the lower turn, but not in the upper. Nuel's space

is not yet to be seen. Deiters' cells become longer, somewhat in the processus phalangeus but chiefly in the cell body, and the nuclei move upward. Hensen's cells also increase in height slightly.

While the membrana tectoria lies close to the surface of the outer part of the greater ridge in the upper turns of the cochlea, there arises a small space between them, which is continuous with the sulcus spiralis internus. The outer marginal zone of the membrane is still connected with Hensen's supporting cells and the lamina reticularis. The vas spirale remains as a large vessel. This is the condition of the nine-day cochlea in a rat which does not hear.

Although the detailed description of the cochlea of the nine-day rat which can hear will be deferred for a time, yet to complete the series of growth changes, figure 8, representing the cochlea in such a rat, is inserted here.

In the next stage, twelve days old (fig. 9), the development of the tympanic wall is much advanced. The cells lining the sulcus spiralis internus and the inner supporting cells have nearly their mature form and arrangement in the basal and middle turns; only in the apical turn many and slender cells remain close to the inner hair cell.

The outer pillar cell shows a remarkable increase in length so that it is twice as long as in the former stage, while the growth of the inner pillar is much less marked.

Therefore the outer pillar is much longer than the inner through all the turns. From this change in the pillar cells it results that the nearly equilateral triangle formed by them becomes unequal and its summit is shifted inward. In all the turns we can see the tunnel of Corti and also the space of Nuel. The hair cells develop further and their previous inclinations are increased.

Deiters' cells show a very rapid development, especially in the cell body, which increases many times, the nucleus moving upwards. The inclination of these cells follows that of the outer hair cells.

Hensen's supporting cells are also fully developed. Through the development of Deiters' and Hensen's cells a change is effected in the course of the lamina reticularis. It runs no longer parallel to the plane of the membrana basilaris, but dips inward.

Though the membrana basilaris remains nearly stationary in its breadth, the thickness of the tympanic covering layer is reduced and the longitudinal nuclei in the zona pectinata diminish in number.

The membrana tectoria reaches in the basal turn to the outermost row of the outer hair cells, but the apical turn only to the second row. The so-called 'outer marginal zone' connects with the terminal frame (Schlussrahmen) of the lamina reticularis.

In the next stage, the twenty-day-old rat (fig.10), the papilla spiralis and the tissues about it are developed almost completely; therefore, the structural relations of the cochlea accord nearly with those of the adult cochlea, as generally recognized in histology.

It is to be noted here that in the basal turn, Böttcher's cells are to be seen in sulcus spiralis externus as a cell group situated on the outer part of the vestibular surface of the membrana basilaris. This cell group consists of several granular compact and sharply bounded cells entirely covered by high swollen cells on all sides. That this cell group belongs to the epithelium of the sulcus spiralis externus can be easily demonstrated. While the cells in this group show no particular changes in structure, the neighboring cells diminish in their height and size towards the apex, and finally become similar to the former. After twenty days of age the general features of the cochlea are those of the adult and do not require general description. The finer differences will be discussed in subsequent chapters.

Figure 11 shows the relations at 100 days and figure 12 at 546 days.

1. Membrana tectoria. As stated above, this membrane is divided into two zones, an outer and inner, using the outer edge of the labium vestibulare as the point of division (fig. 1, 7–7′). Each zone was again divided into two equal parts at 6–6′and8–8′. Thus the sum of the breadths of the two outer parts represents

in each instance the breadth of the outer zone, and the sum of the two inner parts that of the inner zone, while the sum of all four parts gives the total radial breadth. For the purpose of the exact measurement of the growth of the membrane, I have, as noted above, projected the sections at 100 diameters and made the determinations on the outlines thus obtained.

In table 4 (charts 2 and 3) are given the values for the total average breadth, as well as for that of each zone, and also the thickness of the membrane, from 1 to 546 days of age. At the bottom of each column are given the ratios of the breadth at 1 to 546, 12 to 546, and 20 to 546 days. While the ratio between 1 and 546 days is 1.7, those from 12 to 546 days and 20 to 546 days diminish to about 1:1.0, that is the membrane at twelve days has attained about its full breadth, and there is only a very gradual increase in its breadth with advancing age. After twelve days similar ratios are found for the separate zones as well.

From 1 to 546 days the ratios for the two zones differ considerably; that for the second zone is 1:1.2 and that for the first is 1:3.6. This is due to the fact that in the cochlea at birth the development of the labium vestibulare is incomplete, even in the basal turn, while at the apex we can very often hardly see the invasion of the mesenchymal tissue in the inner part of the greater epithelial ridge.

At every stage the outer zone is broader than the inner; the ratio between them at birth is 1:3.8. This diminishes to 1:1.25 at twelve days, after which age it remains practically constant. Owing to the form of the membrana tectoria and to its great sensitiveness to the method of preparation, it is difficult to obtain good values for its thickness.

Generally speaking, the membrane is thickest about midway between the outer edge of the labium vestibulare and the inner boundary of the inner hair cell, and it was here the measurements given in table 4 were made. As shown in this table, the thickness increases rather rapidly from birth to twenty days, but after that period remains approximately constant.

As we know, the radial breadth of the membrane increases gradually from the basal to the apical turn. Table 5 (charts 4, 5, and 6) shows how the breadth of the total and of each part of the membrane changes in successive turns from base to apex according to age. At birth it is broadest in the beginning of the middle turn (turn II) decreasing gradually towards the apex. From three to twenty days the greatest breadth is usually found

TABLE 4

Average radial breadth of the membrana tectoria and its thickness in radial-vertical section. Averages of all four turns (charts 2 and 3)

AGE	BODY WEIGHT	BODY LENGTH	Outer zone between free end of membrane and labium	Inner zone labium vestibulare and insertion of membrane	Total length of membrane	Ratios inner and outer zone	Thickness membrane
days	*grams*	*mm.*	*μ*	*μ*	*μ*		*μ*
1	5	48	140	37	177	1 : 3.78	12
3	8	56	134	94	228	: 1.43	32
6	11	63	154	105	259	: 1.44	32
9	10	58	158	123	281	: 1.28	27
12	13	60	157	126	283	: 1.25	25
15	13	75	160	124	284	: 1.29	28
20	29	95	162	129	291	: 1.26	38
25	36	104	162	128	290	: 1.27	34
50	59	125	162	131	293	: 1.24	35
100	112	159	162	132	294	: 1.23	36
150	183	190	161	131	292	: 1.23	32
257	137	175	163	129	292	: 1.26	38
366	181	191	162	131	293	: 1.24	35
546	255	213	163	132	295	: 1.23	34
Ratios 1 — 546 days			1 : 1.2	1 : 3.6	1 : 1.7		1 : 2.8
12 — 546 "			: 1.0	: 1.0	: 1.0		: 1.4
20 — 5 "			: 1.0	: 1.0	: 1.0		: 0.9

in turn III, but after this in turn IV. At the bottom of each column are given the ratios of the radial breadth in each turn between the several age limits.

These show that after twelve days there is but little change in the radial breadth of the entire membrane in any turn.

On examining the growth in each zone of the membrane through the several turns, we find that after three days the outer zone of the membrane becomes at each age always broader from base to apex.

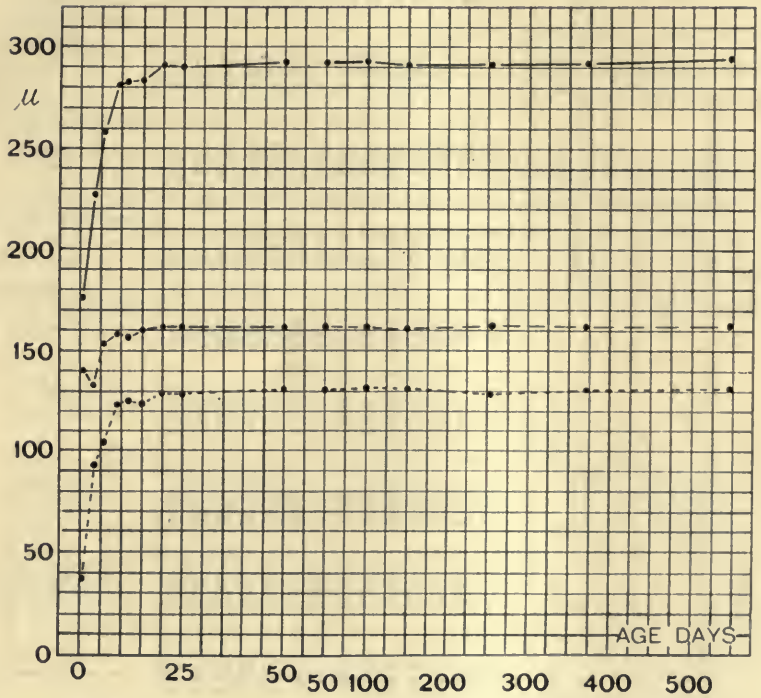

Chart 2 The radial breadth of membrana tectoria, table 4, figure 1.
——— Total radial breadth of the membrane.
..... Radial breadth of outer zone.
– – – – – Radial breadth of inner zone.

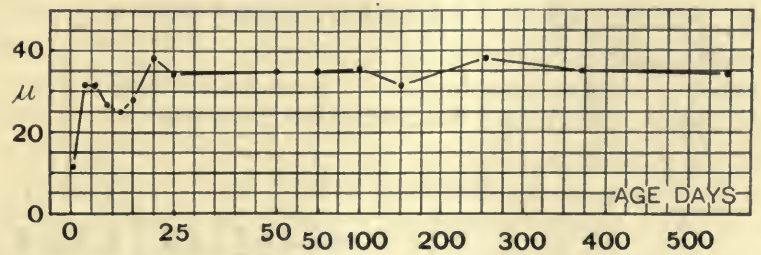

Chart 3 The thickness of membrana tectoria, table 4.

TABLE 5

Radial breadth of the membrana tectoria according to turns of the cochlea—in μ (charts 4, 5, and 6)

AGE	BODY WEIGHT	I			II			III			IV		
		ZONES		TOTAL LENGTH	ZONES		TOTAL LENGTH	ZONES		TOTAL LENGTH	ZONES		TOTAL LENGTH
		Outer	Inner		Outer	Inner		Outer	Inner		Outer	Inner	
days	*gms.*												
1	5	114	64	178	136	48	184	146	34	180	162	0	162
3	8	86	112	198	122	100	222	158	88	246	168	76	244
6	11	104	108	212	142	106	248	176	114	290	192	90	282
9	10	105	138	243	144	126	270	186	118	304	198	108	306
12	13	100	139	239	134	126	260	189	131	320	204	109	313
15	13	104	136	240	145	125	270	188	126	314	203	108	311
20	29	104	140	244	146	132	278	188	133	321	208	112	320
25	36	104	137	241	143	130	273	190	130	320	210	117	327
50	59	105	142	247	147	133	280	189	133	322	206	116	322
100	112	104	141	245	142	132	274	191	130	321	210	124	334
150	183	107	142	249	142	131	273	190	130	320	207	123	330
257	137	106	140	246	147	130	277	188	132	320	209	113	322
366	181	107	141	248	147	133	280	189	127	316	205	122	327
546	255	105	144	249	147	135	282	190	129	319	209	118	327
Ratios													
1–546 days		1 : 0.9	1 : 2.2	1 : 1.4	1 : 1.1	1 : 2.8	1 : 1.5	1 : 1.3	1 : 3.8	1 : 1.8	1 : 1.3	0	1 : 2.0
3–546 "		: 1.2	: 1.3	: 1.3	: 1.2	: 1.4	: 1.3	: 1.2	: 1.5	: 1.3	: 1.2	1 : 1.6	: 1.3
12–546 "		: 1.1	: 1.0	: 1.0	: 1.1	: 1.1	: 1.1	: 1.0	: 1.0	: 1.0	: 1.0	: 1.1	: 1.0
20–546 "		: 1.0	: 1.0	: 1.0	: 1.0	: 1.0	: 1.0	: 1.0	: 1.0	: 1.0	: 1.0	: 1.1	: 1.0

The values at birth are relatively greater than those at three days, as noted above, due to the undevelopment of the labium vestibulare. The inner zone grows in a like manner in breadth, but not so rapidly as the outer zone, and hence its relative breadth diminishes gradually from base to apex.

Table 6 shows these relations. While the ratios in the inner zone decreases from base to apex, those in the outer zone increase. Thus the ratios in the inner and outer zones according to the turns go in opposite directions. As stated above, the radial breadth is generally larger in the outer zone, but this relation is, in general, reversed in turn I, table 5.

TABLE 6—*Condensed*

Ratios of the radial breadth of each zone of the membrana tectoria

AGE	BODY WEIGHT	Ratios according to turns of the cochlea									
		INNER ZONE			OUTER ZONE			Ratios between inner and outer zone			
		Turns			Turns			Turns			
		I–II	I–III	I–IV	I–II	I–III	I–IV	I	II	III	IV
days	*grams*										
1	5	1:0.8	1:0.5	1:0.0	1:1.2	1:1.3	1:1.4	1:1.8	1:2.8	1:4.3	1:0.0
8	11	:0.9	:0.9	:0.8	:1.4	:1.8	:1.9	:0.8	:1.2	:1.6	:2.0
18	21	:0.9	:0.9	:0.8	:1.4	:1.8	:2.0	:0.8	:1.1	:1.5	:1.9
203	160	:0.9	:0.9	:0.8	:1.4	:1.7	:2.0	:0.8	:1.1	:1.5	:1.8

In turn I the average ratios are, after eight days, smaller than 1.0; therefore, the inner zone is wider than the outer in turn I. It increases in all ages from turn II toward the apex.

In table 7 are given the ratios between each turn of the cochlea. The ratios after nine days of age are practically constant according to age, but those between turns I and II are always smaller than the others; the ratios for the two latter being alike. The ratio at one day is, however, an exception, as stated already.

As the measurements show, the membrana tectoria is at birth relatively undeveloped; it is thin and immature. After birth it increases rapidly during the first nine days, a statement which applies generally to the postnatal growth of the organs of the albino rat. Thus we get a ratio of the radial breadth 1:1.7 between 1 and 546 days, but after twelve days the ratios remain practically 1:1.0. (Table 4.)

It is not my purpose to describe the fetal development of the membrana tectoria, but it is worth while to consider briefly the zones which compose the membrane; in other words, the parts of the tympanic wall from which it originated. There are chiefly

TABLE 7

Ratios of the radial breadth of the membrana tectoria according to the turns of the cochlea

AGE	BODY WEIGHT	Ratios according to turn of the cochlea		
		I–II	I–III	I–IV
days	*gms.*			
1	5	1 : 1.0	1 : 1.0	1 : 0.9
3	8	: 1.2	: 1.2	: 1.2
6	11	: 1.2	: 1.4	: 1.3
9	10	: 1.1	: 1.3	: 1.3
12	13	: 1.1	: 1.3	: 1.3
15	13	: 1.1	: 1.3	: 1.3
20	29	: 1.1	: 1.3	: 1.3
25	36	: 1.1	: 1.3	: 1.4
50	59	: 1.1	: 1.3	: 1.3
100	112	: 1.1	: 1.3	: 1.4
150	183	: 1.1	: 1.3	: 1.3
257	137	: 1.1	: 1.3	: 1.3
366	181	: 1.1	: 1.3	: 1.3
546	255	: 1.1	: 1.3	: 1.3

Chart 4 The total radial breadth of membrana tectoria arranged according to the turns of the cochlea, table 5.

———— About middle part of the basal turn (I).

-.-.-.-.-. About the beginning of the middle turn (II).

---------- About the middle part of the middle turn (III).

. . . . . About the beginning of the apical turn (IV).[2]

Chart 5 The radial breadth of the inner zone of the membrana tectoria, according to the turns of the cochlea, table 5.

Chart 6 The radial breadth of the outer zone of the membrana tectoria, according to the turns of the cochlea, table 5.

[2] In most cases when the values which have been determined are analyzed according to the turns of the cochlea, it is found that they increase with later growth from the basal (I) to the apical (IV) turn and in the order just given in chart 4. Owing to this uniformity of behavior, some thirteen charts showing the several values according to turn have been omitted, since the graph given by the average value is sufficiently informing in each instance.

In the case of those charts which have been retained, and in which the measurements are according to the turns of the cochlea, the respective turns I–IV are recorded by characteristic lines similar to those used for them in chart 4, and in these cases the further designations of the turns are omitted.

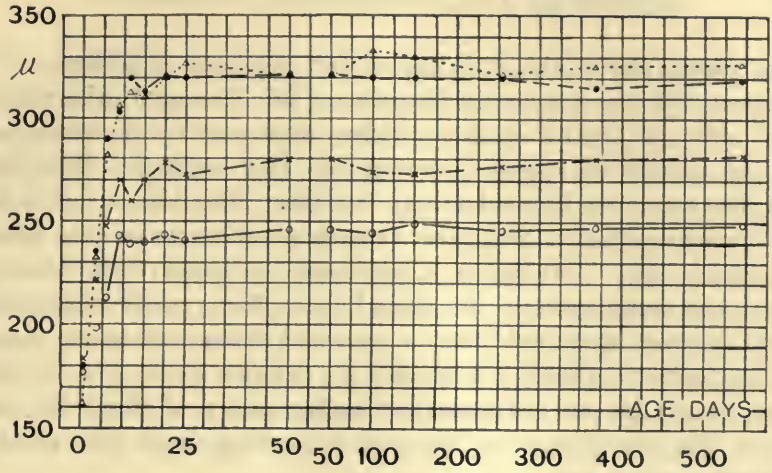

Chart 4

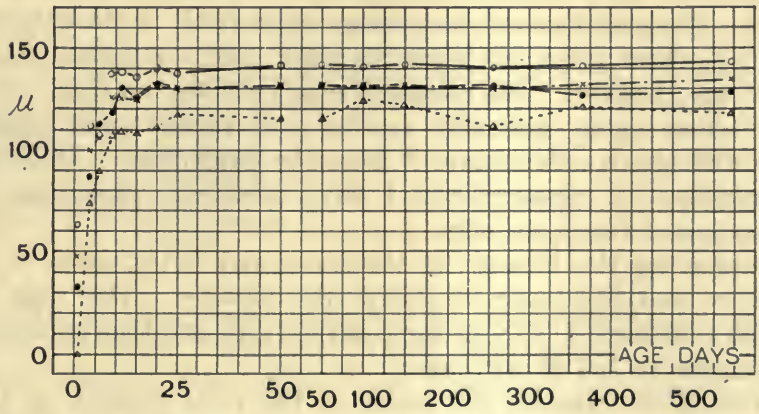

Chart 5

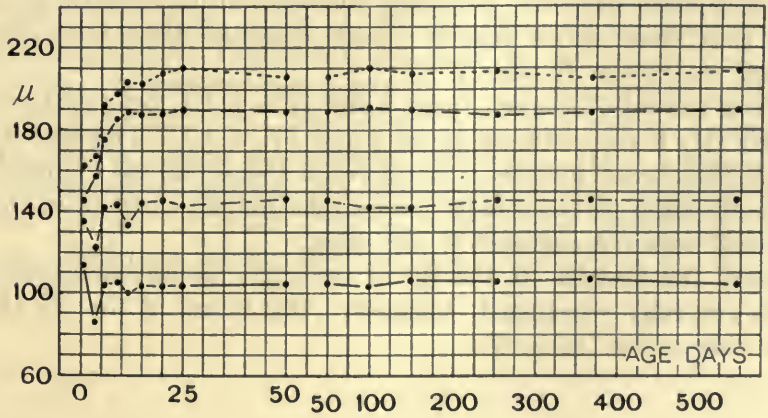

Chart 6

two views about this. While a few authors, Kölliker ('67), Hensen ('63), and recently Hardesty ('08, '15), and others hold that only the greater epithelial ridge takes part in the formation of the membrane, most investigators (for example, Böttcher, '69; Retzius, '84; Rickenbacher, '01; Held, '09; Van der Stricht, '18) consider that it originates from both the greater and lesser epithelial ridge. My figure 5, supports the latter view; that is, while the main part is developed from the greater ridge, the outer narrow marginal part is secreted from the lesser ridge.

The figure in Quain's Anatomy by Schäfer ('09) (vol. 3, part 2, p. 332, 11th ed.,) is from the earlier paper of Hardesty and shows the membrane in the pig as arising from the greater epithelial ridge only.

Hardesty has corrected this figure in his paper published in 1915. Thus in the very early stage after birth in these forms we have three zones, an inner, an outer, and a marginal zone. With age, however, this marginal zone becomes, as Held ('09) and others agree, gradually smaller and smaller, and finally it is difficult to differentiate it from the outer zone. Thus for convenience in measurements I have treated the membrane as consisting of two zones only.

Comparing the breadth of the inner and outer zones, it is evident that the outer is always the broader. The ratio is (table 4) at birth 1:3.78, at three days 1:1.43, and then gradually diminishes to 1:1.23 with age.

Now if we examine the ratios of the total breadth of the membrane according to the turns of the cochlea, we find after six days that the ratio generally increases from base to apex, and that these ratios remain nearly constant after nine days of age, as shown in table 7.

Thus the ratio between turns I and II is 1:1.1; between turns I and III, 1:1.3; between turns I and IV, 1:1.3. The breadth of the membrane increases, therefore, in the albino rat gradually from the base to the middle part of the middle turn; from this point it does not increase to the apex.

Since the breadth at the tip of the apex diminishes greatly, as is generally recognized, Hardesty ('08) found in the pig the following ratios (table 8):

Comparing these ratios obtained by Hardesty in the pig with mine, there appear to be large differences between them. The reason for these I will discuss later.

When we consider the breadth in each part of the membrane according to the turn, we find that the increase of the breadth of the membrane in each turn is due to the development of the outer zone. The inner zone, which is adherent to the labium vestibulare, does not increase in the rat as Hardesty ('08,'15) found to be the case for the pig, but on the contrary decreases from base to apex—a relation found by Retzius ('84) in the rabbit, cat, and man and confirmed by Rickenbacker ('01) in the guinea-pig. On the contrary, the outer zone increases in breadth from

TABLE 8

Ratios of the breadth of the membrana tectoria according to turn of cochlea (Hardesty)

Kind of animal	Preparation method	Ratios between breadth in 7 and 5 half turn	Ratios between 7 and 3 half turn	Ratios between 7 and 1 half turn
Pigs two weeks of age	Membrane teased out	1 : 1.4	1 : 1.7	1 : 2.5
Adult	Membrane teased out	1 : 1.8	1 : 2.5	1 : 2.7
	Membrane in section	1 : 1.6	1 : 2.1	1 : 1.8

base to apex, and in each stage the ratios between the successive turns are nearly the same. These ratios between successive turns, however, show rather large differences according to the different authors.

My results (table 5) show that the outer zone in the albino rat is nearly two times wider at the apex than at the base. This agrees with what von Ebner ('02) finds in the human cochlea.

When we consider the thickness of the membrane, we find it thin at birth, but at three days (table 4) it increases rapidly and reaches almost its greatest thickness. This increase in thickness arises through the apposition of new layers to the under surface, as Hasse ('73) and others have noted, but very large differences appear between the figures given by various authors.

Kölliker ('67) finds the membrane 45 μ thick in the ox. In the guinea-pig it is 15 μ in the thickest place, according to Schwalbe ('87). Middendorp ('67) gets in mammals generally a very thin membrane, about 1 μ thick. Retzius ('84) states that in the thickest part in the rabbit it measures 27 μ, in the cat 32 to 50 μ, and in man 24 to 25 μ. Hardesty finds in the young pig an average thickness of the teased membrane of 50 μ and in an adult hog 119.3 μ. I get 35 μ as an average in the adult albino rat after twenty days of age, varying from 32 to 38 μ. My result is therefore closest to that for the cat as obtained by Retzius. These results are plainly influenced by the dissimilar technical methods used by the several investigators.

About the outermost end of the membrane there are still two different views. One view is that the outer end of the membrane projects beyond Hensen's prominence; Kolmer ('07; pig, calf goat and horse); Hardesty ('15; pig, hog) Shambaugh ('10; pig). Others assert that the membrane terminates with its outer edge at the outer boundary of the outermost series of the outer hair cells. My preparations show that in the rat the outer end of the membrane does not reach Hensen's prominence.

Possibly this difference is due to the technique of preparation. In the figures drawn by many authors we can recognize many artifacts and postmortem changes in the cochlea. Even in the figures of Kolmer ('07) we see these changes, although he injected the fixing solution through the carotid artery. Held ('09) says in his criticism of Hardesty's figures that "figures 6 and 7 wie schon Hardesty selbst vermutet hat, sicherlich auf einer Verquellung beruhen....."

I myself never observed such a gigantic membrane as Hardesty ('08, '15), Shambaugh ('10), and others show in the cochlea of the pig. On the other hand, I cannot absolutely deny that there may have been shrinkage in the cochleas prepared by my methods, though I see no evidence of it.

From our present knowledge, however, the method of vital fixing is considered the best available, as already maintained by Siebenmann and Yoshii ('08), Metzner and Yoshii ('09), Nager and Yoshii ('10), Wittmaack and Laurowitsch ('12), and others.

By using this vital-fixation method we get perfect sections which can be used to solve the problem of the shifting of the organ of Corti—an event which I will discuss later.

2. Membrana basilaris. The membrana basilaris of the cochlea stretches between the limbus laminae spiralis and the ligamentum spirale. The acoustic terminal apparatus is situated on it and according to the dominant Helmholtz-Hensen theory, this membrane is to be considered as very important in tone perception. The row of the fine holes, foramina nervina, is generally designated as the inner boundary of this membrane. Strictly speaking, however, the beginning of the membrane is at the outer edge of the labium tympanicum, which sharpens at first beyond the foramina nervina and passes over to the substance of the membrana basilaris. Practically it is almost impossible to decide exactly the point of transition. Thus I have used in the measurement of the membrane the foramina of the habenula perforata as an inner limiting line following in this Retzius, ('84) Schwalbe ('87), and others. Here it is to be mentioned that the organ of Corti lies with its inner portion not only upon the inner part of the membrane, but extends to the foramina nervina also.

The membrana basilaris is usually divided into two portions; the inner, termed the zona arcuata, and the outer, the zona pectinata. The former stretches from the habenula perforata across the base of the tunnel of Corti to the outer edge of the foot of the outer rods of Corti; the latter extends from this point to the ligamentum spirale (fig. 2), 5=inner zone, 10=outer zone.

In table 9 (chart 7) are given the values for the total radial breadth of the membrane, that of each zone, and the ratios between them. At the bottom of each column are given the ratios at 1 to 546, 12 to 546, and 20 to 546 days of age. In the total radial breadth of the membrane, as the table shows, there are large differences on age from birth to nine days. Between 1 day and three days the increase is 30 μ and between three days and six days, 28 μ. After nine days the breadth increases more slowly but continuously to old age.

In the growth of both zones we see about the same relation. These increase rapidly from birth till nine (or twelve) days and after that very slowly. These relations are shown clearly in the ratios at 1 to 546, 12 to 546, and 20 to 546 days. While after twelve days the ratios in total breadth and in each zone are the same, 1:1.1, that for 1 to 546 days is smaller for the outer zone than it is for the inner zone, thus the inner zone increases

TABLE 9

Radial breadth of the membrana basilaris measured between the foramina nervina and ligamentum spirale in radial sections—on age (chart 7, fig. 2)

AGE	BODY WEIGHT	INNER ZONE (Zona arcuata)	OUTER ZONE (Zona pectinata)	Total radial breadth of the membrane	Ratios between the radial breadth of the inner and outer zone
days	*grams*	*μ*	*μ*	*μ*	*μ*
1	5	49	75	124	1 : 1.5
3	8	63	91	154	: 1.5
6	11	77	105	182	: 1.4
9[1]	10	79	111	190	: 1.4
12	13	88	100	188	: 1.1
15	13	87	102	189	: 1.2
20	29	86	106	192	: 1.2
25	36	87	108	195	: 1.2
50	59	88	107	195	: 1.2
100	112	92	106	198	: 1.2
150	183	92	107	199	: 1.2
257	137	92	107	199	: 1.2
366	181	93	111	204	: 1.2
546	255	94	113	207	: 1.2
Ratios 1 —546 days		1 : 1.9	1 : 1.5	1 : 1.7	
12—546 "		: 1.1	: 1.1	: 1.1	
20—546 "		: 1.1	: 1.1	: 1.1	
[1] A rat of nine days which could hear, gave the following:					
Right side	11	94	103	197	
		91	104	195	
		93	104	196	1 : 1.1

considerably after birth, while the outer zone does not grow, as some authors have imagined, as much as the inner zone. I will discuss this point later.

Comparing the growths of the radial breadth of the inner and outer zones, we find that the inner zone is relatively narrow at nine days; thus the ratios between them are 1:1.4; after that period the inner zone increases rapidly, and even at twelve days the ratio becomes 1:1.1, which is almost the same as in the adult, 1:1.2.

In table 10 the radial breadths of the whole membrane and of its zones are arranged accordingly to the turns of the cochlea on age. At the bottom of each column are given the ratios from 1 to 546, 12 to 546, and 20 to 546 days. We see at first that the total radial breadth at one day is largest in the basal turn; at three days it becomes larger on passing from the basal toward the II and III turns, but in turn IV it is again small.

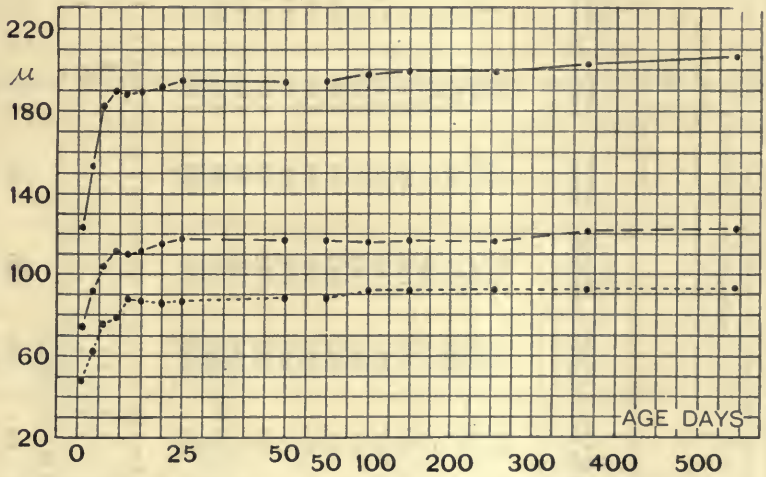

Chart 7 The radial breadth of the membrana basilaris, table 9, figure 2, distance 11.

———— Total radial breadth of the membrane.
---------- Radial breadth of the zona pectinata.
..... Radial breadth of the zona arcuata.

After six days it is a well-known fact that the radial breadth of the membrana basilaris is narrowest in the basal, and widest in the apical turn (not the tip of the apex, but the beginning of the apical turn). These differences are not always the same between all the turns; those between I and II, and II and III are marked; those between III and IV are small. The ratios at 1 to 546 days show those for the upper turn to be largest, while from 12 to 546, and 20 to 546 days the ratios in all turns are about 1:1.1.

TABLE 10

Radial breadth of the membrana basilaris of the cochlea arranged according to turns—on age

AGE	BODY WEIGHT	TURNS OF THE COCHLEA μ											
		I			II			III			IV		
		INNER ZONE	OUTER ZONE	TOTAL RADIAL BREADTH	INNER ZONE	OUTER ZONE	TOTAL RADIAL BREADTH	INNER ZONE	OUTER ZONE	TOTAL RADIAL BREADTH	INNER ZONE	OUTER ZONE	TOTAL RADIAL BREADTH
days	*grams*												
1	5	50	76	126	50	76	126	48	73	121	50	74	124
3	8	63	91	154	65	92	157	64	93	157	58	89	147
6	11	64	98	162	73	104	177	86	109	195	86	109	195
9[1]	10	70	99	169	76	113	189	86	116	202	86	116	202
12	13	69	87	156	83	98	181	98	106	204	100	111	211
15	13	70	92	162	84	101	185	98	106	204	95	109	204
20	29	71	95	166	81	103	184	96	111	207	97	115	212
25	36	71	96	167	88	105	193	95	114	209	97	116	213
50	59	69	97	166	83	103	186	96	114	210	103	114	217
100	112	73	96	169	88	102	190	101	113	214	106	113	219
150	183	73	98	171	90	102	192	98	113	211	107	116	223
257	137	76	96	172	87	104	191	98	114	212	107	114	221
366	181	76	99	175	89	107	196	100	118	218	107	122	229
546	255	78	103	181	89	109	198	104	119	223	106	120	226
Ratios													
1–546 days		1 : 1.6	1 : 1.4	1 : 1.4	1 : 1.8	1 : 1.4	1 : 1.6	1 : 2.2	1 : 1.6	1 : 1.8	1 : 2.1	1 : 1.6	1: 1.8
12–546 "		: 1.1	: 1.2	: 1.2	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1
20–546 "		: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.1	: 1.0	: 1.1
[1] A nine day old rat which could hear gives the following:													
Right side	11	80	90	170	88	98	186	105	113	218	103	113	216
Left side		78	95	173	88	100	188	100	110	210	100	113	213
Average				172			187			214			215

In the zona arcuata (inner zone) the same relation is to be seen in each turn; therefore, in the early period the breadth is less in turn IV than in the other turns. Very soon, however, the value in turn IV becomes the largest and diminishes toward the base. The rate of the growth of this zone, from 1 to 546 days, is also smallest in turn I, and largest in turns III or IV; the ratios being in the first 1:1.6, and in the last 1:2.1.

In the zona pectinata (outer zone) we see also similar relations.

TABLE 11

Ratios of the radial breadth of the membrana basilaris according to the turns of the cochlea—on age

AGE	BODY WEIGHT	Ratios between turns		
		I–II	I–III	I–IV
days	*gms.*			
1	5	1 : 1.0	1 : 1.0	1 : 1.0
3	8	: 1.0	: 1.0	: 1.0
6	11	: 1.1	: 1.2	: 1.2
9	10	: 1.1	: 1.2	: 1.1
12	13	: 1.2	: 1.3	: 1.3
15	13	: 1.1	: 1.3	: 1.3
20	29	: 1.1	: 1.2	: 1.3
25	36	: 1.2	: 1.3	: 1.3
50	59	: 1.1	: 1.3	: 1.3
100	112	: 1.1	: 1.3	: 1.3
150	183	: 1.1	: 1.2	: 1.3
257	137	: 1.1	: 1.2	: 1.3
366	181	: 1.1	: 1.2	: 1.3
546	255	: 1.1	: 1.2	: 1.3

Only slight differences in the ratios according to age are found.

In table 11 the ratios according to the turns of the cochlea are given. While from one to three days the ratios are the same in each turn, 1:1.0, yet after six days those for turns I to II are smallest, and for I to IV larger, thus showing slight differences between them.

In the literature we find only one description, that by Retzius ('84) touching the growth of the radial breadth of the membrana basilaris according to age. He measured this membrane in the rabbit and cat and got the following values in μ (table 12).

Comparing these values with mine obtained for the albino rat, it is to be noted that those of Retzius are generally larger than those for the albino. For example, while I get at birth only 126 μ in the basal turn, Retzius ('84) obtains 180 μ in the rabbit and even 270 μ in the cat. As stated above, the radial breadth increases in the albino rat continuously with age. It is very peculiar to find in the Retzius table that the breadth of the membrane in the cat is decidedly larger at birth than at three and seven days. The average value for the new-born is 315 μ, which is larger than at thirty days, which is 310 μ.

Retzius' data show the membrane in the rabbit and cat always wider in the apical than in the basal turn at birth and at two

TABLE 12

Breadth of membrana basilaris according to turns, μ. (From Retzius, '84)

	RABBIT			CAT		
Age	Basal	Middle	Apical	Basal	Middle	Apical
days						
New-born	180	270	—	270	300	375
2	220	272	280	—	—	—
3	—	—	—	200	280	—
7	270	306	—	211	258	300
10	255	310	390	—	—	—
11	—	—	—	255	300	330
14	300	360	410	—	—	—
30	—	—	—	240	300	390

days. My results, given in table 10, show the reverse at the ages of one and three days. This is an expression of greater immaturity in the case of the rat.

In comparisons like the foregoing, several conditions must be kept constantly in view.

So far as absolute values are concerned, it is to be expected that these would be unlike in the different mammals, because the cochleas differ in size. As to the relations between the values at birth and at maturity, it is plain that these cannot be expected to agree unless the cochleas of the animals compared are in the same phase of development at birth. In the foregoing instances it appears that the cat is relatively precocious, as compared with the rabbit, while, as might be expected, because

of their closer zoological relationship, the rat and the rabbit are in better agreement, although the rabbit appears to be a trifle more advanced at birth than the rat.

Finally, in the comparison of different series of data, differences due to the lack of homogeneity in the series of animals used and to the various techniques employed can hardly fail to play an important part, and allowance must be made for these disturbing factors.

When we consider the rate of growth, the ratio of a one to a fourteen-day-old rabbit is 1:1.6, according to Retzius; therefore,

TABLE 13

Breadth of basilar membrane

ANIMAL AUTHOR	TURN IN WHICH MEASUREMENT WAS MADE IN μ				
	Basal	Second	Third	Fourth	Average
Man-New-born Hensen ('63)	235	413		495	381
Man—Mature Retzius ('84)	210		340	360	303
Calf Kolmer ('07)	200	280		400	293
Pig Kolmer ('07)	168	200	256	304	232
Goat Kolmer ('07)	124	384	432		313
Cat Böttcher ('69)	90		435		263
Cat Middendorp ('67)					246–275

it has very nearly the value found in the albino. In the cat, however, the ratio between one and thirty days is 1:0.97; therefore, it apparently decreases a bit.

This difference is most readily explained as due to the precocious development in the cat at birth.

On comparing the radial breadth of the membrane obtained from several mammals by various authors, we find the following values (table 13).

The values here given must be read in the light of the various modifying conditions to which reference has just been made.

My average value after twenty days is 199 μ; therefore, it is absolutely the smallest in this series of mammals. The rat is also the smallest species examined.

As shown in the literature quoted, and also in my own results, the membrane increases in its breadth in all the mammals examined from the base toward the apex—a relation contrary to that reported by the older authors (Corti, '51, and others). This increase is continuous, but is at first more rapid and afterwards more gradual. The ratios of this increase in the albino rat are given in table 11.

The next question relates to the breadth of each zone of the membrane according to age. So far as I know, there is no such study in the literature, not even in Retzius. In the albino rat, as shown in table 9, each zone increases in breadth with age. The rate of growth, however, is somewhat different, and in the zona arcuata it is greater than in the zona pectinata (1:1.9 and 1:1.5, respectively), although the absolute value is always greater in the latter.

As noted above, the membrane increases in its radial breadth from the basal to the apical turn. How, and in which portion of the membrane does this increase arise? Henle ('66) first regarded the breadth of the inner (zona arcuata) as approximately constant.

"Nicht nur in den verschiedenen Regionen einer Schnecke, sondern, soviel ich sehe, selbst in den Sshnecken verscheidener Tiere und des Menschen; sie schwankt nur wenig um 0.01 mm." (Eingeweidelehre des Menschen, 1866, S. 793).

In the second edition of his book ('73) he states, however, that in the increase of the breadth according to the turn, both zones seem to take part. Hensen ('63) gets in the zona arcuata of the base of the human cochlea the breadth of 19 μ and in the apex 85 μ. Middendorp ('68) gives in the cochlea of the cat a continuous increase of the breadth of the zona arcuata from 94 to 122.5 μ.

More detailed data are given in table 14.

According to all these authors, the breadth of both the inner and outer zones increases from base toward apex and results

in the increase of the total radial breadth of the membrane according to turn. My results obtained from the albino rat agree with these data.

3. Radial distance between the habenula perforata and the inner corner of the inner pillar cells at base. The measurements of the radial distance from the habenula perforata to the bases of the inner and outer pillar cells were taken to determine their postnatal growth. As already stated, the cells from which the arch of Corti arises stand at birth nearly vertically and have no space between them (fig. 4). In the adult, however (fig. 10), we see a space, the tunnel of Corti lying between them and changes in the form of the arch occur. To follow these changes

TABLE 14

Breadth of the inner zone of the membrana basilaris in μ

	NUMBER OF TURN			
	First	Second	Third	Fourth
Cat-adult				
Böttcher ('69)	60	105	135	
Guinea-pig				
Winiwarter ('70)	45–52	63–68	71–80	80–83

it seems at first necessary to study the growth of the pillar cells and of the other elements in the organ of Corti. At the same time we must take into consideration the inward shifting of the organ of Corti, first studied by Hensen. This shift inward of the organ is, according to Hensen, chiefly caused by the wandering of the pillar cells, especially the inner pillar cell. Therefore, it seemed necessary to determine the radial distance of the pillar cells from the habenula perforata at different ages before discussing this interesting problem.

In table 15 are given the values for the radial distances between the habenula perforata and the inner corner of the inner pillar cell at its base according to age (figs. 4 to 9). As we see, the average value increases till three days of age, then vanishes suddenly, though at six days we have a measurable interval in the upper turns of the cochlea. Comparing these distances according to the turn, they are smallest in turn I and increase

toward the apex. In some cases, at six days, we have no interval in the basal turn, but in the higher turns an interval gradually appears and at the apical turn is largest. This table shows, therefore, that the inner corner of the base of the inner pillar cell lies at birth outward from the habenula perforata at an

TABLE 15—*Condensed*

Radial distance between the habenula perforata and the inner corner of the inner pillar at base—on age

AGE	BODY WEIGHT	TURNS OF THE COCHLEA μ				
		I	II	III	IV	Aver.
days						
1	5	19	22	22	23	22
3	8	23	28	28	30	27
6	11	In one case 5 In other 3 cases 0	In 2 cases 10 In other cases 0	14	18	—
9	10	0	0	0	0	0
12	13	0	0	0	0	0

average distance of 22 μ. At three days of age the inner corner moves farther outward with the developing membrana basilaris and the distance increases from the base to the apex. Between three to six days this outward movement not only stops, but reverses its direction, and at six days it often becomes zero in the basal turn. Böttcher ('72) finds in the cat the following values for this interval in μ (table 16).

TABLE 16

CAT EMBRYO—11 CM. LONG					ADULT CAT				
I	II	III	IV	Average	I	II	III	IV	Average
15	39	30	30	29	3	3	3	3	3

TABLE 17

AGE	RABBIT				CAT			
	Basal turn	Middle	Apical	Average	Basal	Middle	Apical	Average
days								
New-born	300	300	300	300	5	40	45	30
2	10	12	30	17	—	—	—	—
3	0	0	0	0	3	36	—	—
7	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	18	—

Retzius ('84) studied this distance in the rabbit and cat and gets the values given in Table 17.

Comparing the values of these two authors with my own, there are of course some differences. While in the rabbit the interval is large at one day, it is greatly diminished at two days of age. At three days the inner corner of the cell reaches the habenula perforata. In the cat the values are nearer to mine. The fact that the values increase from base toward apex is to be seen here also. This peculiar phenomenon appears, therefore not only in the albino rat, but also in the rabbit and the cat during the earliest stage of postnatal life.

4. The radial distance between the habenula perforata and the outer corner of the inner pillar cell (resp. the inner corner of the outer pillar cell) at base. This measurement is difficult. As we know, the inner and outer pillar cells in the albino are from birth till nine days of age in contact with each other along their whole length, and therefore they do not yet surround the space forming the tunnel of Corti. At about nine days, however, the tunnel appears while the cells remain in contact by their bases. It is almost impossible to determine the line of contact on the basilar membrane in my preparations. To get the radial distance between the habenula perforata and the outer corner of the inner pillar cell I have proceeded therefore as follows:

First, I have measured this distance directly up to nine days of age; after that this distance consists of the sum of the radial basal breadth of the inner pillar (not pillar cell) and the breadth of the inner basal cell on the basilar membrane. Since it is impossible to get the latter value directly in my sections, I considered that half of the radial distance between the outer corner of the inner pillar and the inner corner of the outer pillar would be equivalent to it.

Of course, I do not know whether the value of the sum of these two distances is at all ages, identical with the distance between the habenula perforata and the outer corner of the inner pillar cell at its base. I believe, however, that a systematic study of the growth of this distance will be significant.

In table 18 are given the values for the radial distance between the habenula perforata and the outer corner of the inner pillar at base up to nine days of age. As shown, these values, on the average, increase with age. The increase of this distance means that the base of the inner pillar cell spreads outward more and more.

When we consider this distance according to the coil of the cochlea, it is at birth about the same through all the turns (table 18; at three days it increases up to turn III, and in turn

TABLE 18

Radial distance between the habenula perforata and the outer corner of the inner pillar at base—on age

AGE	BODY WEIGHT	TURNS OF COCHLEA μ				
		I	II	III	VI	Average
days	*grams*					
1	5	40	41	39	39	40
3	8	48	49	50	48	48
6	11	38	45	58	53	49
9	10	44	46	56	53	50

IV the value is the same at the apex as at the base. At six days the value in turn III is also largest, and next largest in turn IV. At nine days of age the same relations are to be seen.

In table 19 (chart 8) are given the values for the radial basal breadth of the inner pillar (not pillar cell) on age. At the bottom of the last column are the ratios from 6 to 546, and 20 to 546 days. As above noted, the rod can be followed at birth from the upper part to near the base of the cell (fig. 4). At three days (fig. 5), its base reaches the basilar membrane as a thin and slender thread, but we cannot measure its basal breadth accurately. During the next few days it increases in radial breadth rapidly, and at six days has the average value of 29 μ (table 19). After nine days it decreases distinctly till twenty days, after which the value remains nearly constant. These relations are evident in the ratios. While the breadth at six days is about twice that at 546 days, that at twenty days has the same value.

According to the turn of the cochlea, the values from nine to fifteen days become gradually larger on passing from the base toward the apex. After twenty days, however, this relation vanishes, and the values become nearly the same through all

TABLE 19

Radial basal breadth of the inner pillar—on age (chart 8)

AGE	WEIGHT BODY	TURNS OF THE COCHLEA μ				
		I	II	III	IV	Average
days	*grams*					
1	5	0	0	0	0	0
3	8	0	0	0	0	0
6	11	29	31	27	27	29
9	10	28	28	33	35	31
12	13	18	19	22	25	21
15	13	18	18	19	19	19
20	29	14	15	15	15	15
25	36	14	15	14	15	15
50	59	14	14	14	13	14
100	112	14	14	14	13	14
150	183	15	15	15	15	15
257	137	15	15	15	15	15
366	181	16	17	15	15	16
546	255	15	14	16	15	15
Ratios 6—546 days						1 : 0.5
20—546 "						: 1.0

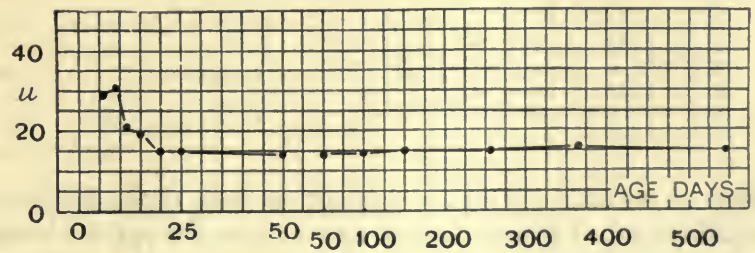

Chart 8. The radial basal breadth of the inner pillar (not pillar cell), table 19, figure 2, distance 3.

the turns. In table 20 the ratios of the turns I to II, I to III, and I to IV are given for three age groups (condensed from table 19)

From the data given by Retzius ('84) we get the values in μ of the radial basal breadth of the inner pillar in the rabbit and cat as follows (table 21).

Comparing these values with my own, it is to be noted that Retzius' measurements in the rabbit agree perfectly at the earliest stage with those in the albino rat. Also we find in the

TABLE 20—*Condensed*

Ratios of the radial basal breadth of the inner pillar according to the turns of the cochlea—on age

AGE	BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
8	11	1 : 1.0	1 : 1.0	1 : 1.1
14	13	: 1.1	: 1.2	: 1.3
189	124	: 1.0	: 1.0	: 1.0

TABLE 21

Radial basal breadth of inner pillar—in μ (Retzius)

	RABBIT				CAT			
Age	Basal turn	Middle	Apical	Average	Basal	Middle	Apical	Average
days								
New-born	0	0	0	0	11	—	—	—
2	0	0	0	0	—	—	—	—
3	—	—	—	—	12	—	—	—
7	15	12	15	14	10	15	—	—
10	17	18	18	18	—	—	—	—
11	—	—	—	—	15	15	—	—
14	15	15	12	14	—	—	—	—
30	—	—	—	—	9	12	15	12

rabbit at seven days values homologous with those obtained in the albino rat at fifteen days of age, only in the rat the breadth is absolutely greater. In the cat the values at seven days of age are about the same, or a bit smaller, than those in the albino rat. Here again the rabbit is a trifle more precocious than the rat, and the cat much more so.

Table 22 (chart 9) shows the values for the radial distance between the outer corner of the inner pillar (not pillar cell)

TABLE 22

Radial distance between the outer corner of the inner pillar and the inner corner of the outer pillar—at base—on age (chart 9)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA μ				
		I	II	III	IV	Average
days	*grams*					
1	5	0	0	0	0	0
3	8	0	0	0	0	0
6	11	25	28	29	34	29
9	10	27	30	35	30	31
12	13	37	41	51	53	46
15	13	35	46	56	56	48
20	29	43	53	66	68	58
25	36	42	58	67	68	59
50	59	41	54	68	74	59
100	112	44	59	71	78	63
150	183	43	59	68	76	62
257	137	46	56	66	75	61
366	181	45	57	68	74	61
546	255	47	60	71	74	63

Ratios 6—546 days 1 : 2.2
12—546 " : 1.4
20—546 " : 1.1

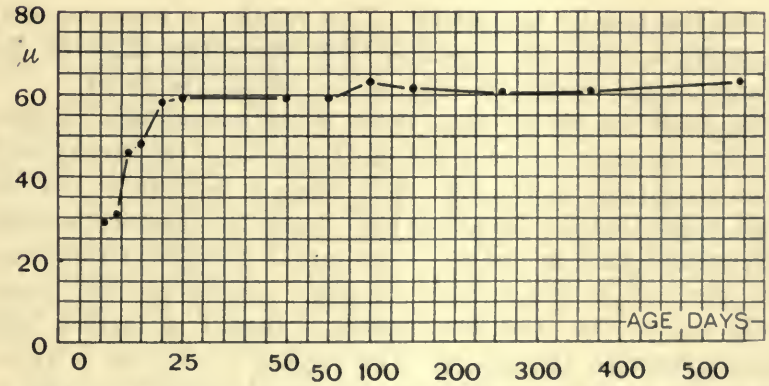

Chart 9. The radial distance between the outer corner of the inner pillar (not pillar cell) and the inner corner of the outer pillar (not pillar cell) at base, table 22, figure 2, distance 6.

and the inner corner of the pillar (not pillar cell) at the base, on age. At the bottom of the last column are given the ratios from 6 to 546, 12 to 546, and 20 to 546 days. As just stated, the inner, and especially the outer rods, do not appear in the respective pillar cells at the earliest stage, the latter becoming evident a bit later than the former. After six days of age the distance between them can be determined.

As table 22 shows, this distance increases at first rapidly, then more slowly with age. This agrees with the growth of the membrana basilaris, as already noted. While the value at 546 days is over twice as large as at six days, it is but little larger than at twenty days, as the ratios show. Moreover, the distance increases from the base toward the apex rapidly up to turn

TABLE 23—*Condensed*

Ratios of the radial distance between the outer corner of the inner pillar and the inner corner of the outer pillar, at base—according to turns of the cochlea—on age

AGE	BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
8	11	1 : 1.1	1 : 1.2	1 : 1.2
14	13	: 1.2	: 1.5	: 1.5
189	124	: 1.3	: 1.5	: 1.7

III and less rapidly to turn IV. This relation is more concisely presented in table 23. Retzius ('84) gives the value of this distance in the rabbit and the cat as follows (table 24).

The table 24 shows that there is no measurable distance between the outer corner of the inner pillar and the inner corner of the outer pillar at the very early stage in the rabbit, and this result is like that for the albino rat. Later the distance is larger in the rabbit than in the rat. The rate of increase of the values from the base to the apex is, however, similar in both forms. In the cat, on the other hand, there is already at birth a large distance between the pillars. The cochlea of the cat is therefore at this period more advanced in this character than that of the rabbit or rat, but in the cat also the distance tends to increase from the base toward the apex.

In table 25 (chart 10) are given the values for the radial distance between the habenula perforata and the outer corner of the inner pillar cell (resp. the inner corner of the outer pillar cell) at the base according to age. This table is derived from tables 18, 19, and 22. The values from one to nine days of age are from table 18. Those after twelve days consist of the sum of the values in table 19 plus the one-half of those given in table 22 (fig. 2 value for bracket 3 plus one-half the value for bracket 6).

TABLE 24

Radial distance between the outer corner of the inner pillar and inner corner of the outer pillar—in μ (Retzius)

	RABBIT				CAT			
Age	Basal turn	Middle turn	Apical turn	Average turn	Basal turn	Middle turn	Apical turn	Average turn
days								
New-born	0	0	0	0	64	—	—	—
2	0	0	0	0	—	—	—	—
3	—	—	—	—	45	—	—	—
7	57	75	75	69	50	75	—	—
10	52	72	74	66	—	—	—	—
11	—	—	—	—	75	95	—	—
14	63	100	99	87	—	—	—	—
30	—	—	—	—	66	93	90	83

The values increase gradually after birth till nine days, when they reach a maximum, and then decrease, but increase again very gradually till old age. If this method of measurement is accepted, then the inner corner of the inner pillar cell lengthens inward at the base in the earlier stages. At the time when the inner pillar reaches the habenula perforata, the outer corner of the inner pillar has not yet moved inward, and thus the breadth of the base is largest. After the inward wandering of the inner pillar cell, the base diminishes a little in its breadth; then it increases slightly with advancing age.

When considered according to the turn of the cochlea, this measurement generally increases from the base to the apex, but more rapidly from turn I to turn III, and only slightly from

TABLE 25

Radial distance between the habenula perforata and the outer corner of the inner pillar cell (resp. the inner corner of the outer pillar cell) at base—on age. Derived from tables 18, 19 and 22 (chart 10)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	40	41	39	39	40
3	8	46	49	49	49	48
6	11	38	45	58	53	49
9	10	44	46	56	53	50
12	13	36	45	50	50	45
15	13	36	41	47	47	43
20	29	36	42	48	49	44
25	36	35	44	48	49	44
50	59	35	41	48	50	44
100	112	36	44	50	52	46
150	183	36	45	49	53	46
257	137	38	43	48	51	45
366	181	39	45	49	52	46
546	255	39	44	52	52	47

Ratios 1—546 days	1 : 1.2
9—546 "	: 0.9
12—546 "	: 1.0
20—546 "	: 1.1

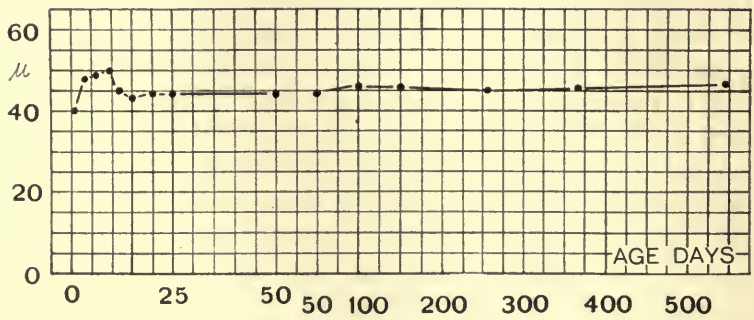

Chart 10 The radial distance between the habenula perforata and the outer corner of the inner pillar cell (resp. the inner corner of the outer pillar cell) at base, table 25, figure 2, distance 8.

turn III to IV. Table 26 shows this relation. While at birth the ratio is in all turns the same, 1:1.0, at other ages it is always higher. Retzius ('84) gives the results obtained from the rabbit and the cat as follows (table 27).

TABLE 26—*Condensed*

Ratios of the radial basal distance between the habenula perforata and the outer corner of the inner pillar cell (resp. the inner corner of the outer pillar cell) at base—on age—according to the turns of the cochlea

AGE	BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.0	1 : 1.0
8	11	: 1.2	: 1.4	: 1.3
18	21	: 1.2	: 1.3	: 1.3
213	138	: 1.2	: 1.3	: 1.4

TABLE 27

Distance between the habenula perforata and the outer corner of the inner pillar cell in μ (Retzius)

	RABBIT				CAT			
Age	Basal turn	Middle turn	Apical turn	Average turn	Basal turn	Middle turn	Apical turn	Average turn
days								
New-born	30	45	39	38	60	60	60	60
2	30	36	30	32	—	—	—	—
3	—	—	—	—	44	60	—	—
7	37	46	45	43	45	69(?)	65	60
10	39	52	48	46	—	—	—	—
11	—	—	—	—	60	66	75	67
14	40	54	51	48	—	—	—	—
30	—	—	—	—	—	60	60	—

At the earlier stage this distance in the rabbit is a little less than in the rat. Soon after, however, it becomes about the same. In the cat the values are generally larger than in the rat.

5. Radial basal breadth of the outer pillar cell (including the outer pillar). The measurement of the radial basal breadth of the outer pillar cell is difficult. At the earlier stage, in which the inner and outer pillar cells are in contact with each other along

TABLE 28

Radial basal breadth of the outer pillar cell (including the outer pillar) from one to nine days of age

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	10	9	8	8	9
3	8	15	16	15	12	15
6	11	26	28	28	33	28
9	10	26	30	30	35	30

TABLE 29

Radial basal breadth of the outer pillar—on age (chart 11)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	0	0	0	0	0
3	8	0	0	0	0	0
6	11	10	14	16	17	14
9	10	15	18	18	21	18
12	13	14	23	25	22	21
15	13	17	21	23	20	20
20	29	13	13	16	15	14
25	36	14	13	14	14	14
50	59	14	14	15	14	14
100	112	14	15	16	15	15
150	183	15	15	15	16	15
257	137	15	16	17	17	16
366	181	15	16	17	18	16
546	255	16	15	17	17	16

Ratios 6—546 days 1 : 1.1
12—546 " : 0.8
20—546 " : 1.1

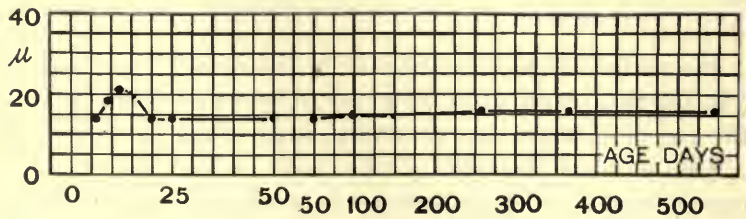

Chart 11 The radial basal breadth of the outer pillar (not pillar cell) table 29, figure 2, distance 7.

their whole length, we can easily measure this distance. After twelve days, however, the breadth consists of the sum of the radial breadth of the outer pillar and the half of the radial distance between the outer corner of the inner pillar and the inner corner of the outer pillar, as previously explained.

In table 28 are given the values for the radial basal breadth of the outer pillar cell (including the outer pillar) from birth to nine days of age. These values show a rapid increase. According to the turn of the cochlea, the breadth at birth diminishes from the base to the apex. At three days it increases already in turn II, but at the later ages it increases gradually from the base to the apex.

TABLE 30—*Condensed*

Ratios of the radial basal breadth of the outer pillars—on age—according to the turns of the cochlea

AGE	BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
8	11	1 : 1.2	1 : 1.3	1 : 1.5
14	13	: 1.4	: 1.5	: 1.3
189	124	: 1.0	: 1.1	: 1.1

In table 29 (chart 11) are given the values for the radial basal breadth of the outer pillar (not pillar cell). As in the case of the inner pillar, here also the outer pillar first appears distinctly at six days of age. After the continuous increase of the values till twelve to fifteen days, they decrease suddenly at twenty days, and then increase again very slowly. This relation is clearly shown by the ratios at the bottom of the last column. That the values tend to increase from the base toward the apex is also shown, though there are some exceptions. Table 30 gives the condensed results.

From Retzius' work ('84) we have calculated the values for the radial basal breadth of the outer pillar in the rabbit and cat as follows (table 31).

There are large differences between my results and those of Retzius during the earlier stage, especially in the rabbit.

At birth, the inner pillar has not yet distinctly developed at the base of the pillar cell in the rabbit and the rat, as above stated. We know that the development of the elements of the cochlea proceeds generally from the axis to the periphery, as

TABLE 31

Radial basal breadth of outer pillar measured in μ (from Retzius)

	RABBIT				CAT			
Age	Basal turn	Middle turn	Apical turn	Average	Basal turn	Middle turn	Apical turn	Average
days								
New-born	15?	12?	7?	11?	25	15	—	—
2	50	45	44	46	—	—	—	—
3	—	—	—	—	20	—	—	—
7	28	28	17	24	18	20	18	19
10	31	30	37	33	—	—	—	—
11	—	—	—	—	30	19	—	—
14	28	25	18	24	—	—	—	—
30	—	—	—	—	10	15	15	13

TABLE 32

Radial basal breadth of the outer pillar cells—on age, based on tables 22, 28, and 29 (charts 12 and 13)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	10	9	8	8	9
3	8	15	16	15	12	15
6	11	26	28	28	33	28
9	10	26	30	30	35	30
12	13	33	38	48	52	43
15	13	35	44	50	48	44
20	29	35	40	49	49	43
25	36	35	42	48	48	43
50	59	35	41	49	51	44
100	112	36	45	52	54	47
150	183	36	45	49	54	46
257	137	38	44	50	53	46
366	181	38	43	51	55	47
546	255	40	45	53	54	48

Ratios 1—546 days	1 : 5.4
9—546 "	: 1.6
12—546 "	: 1.1
20—546 "	: 1.1

Held ('09) and others have pointed out. Yet, according to Retzius, the outer pillar develops in the rabbit earlier than does the inner pillar. This result seems to me very peculiar, but, at present, I am unable to explain it.

In table 32 (charts 12 and 13) are given the values for the radial basal breadth of the outer pillar cells. These data are

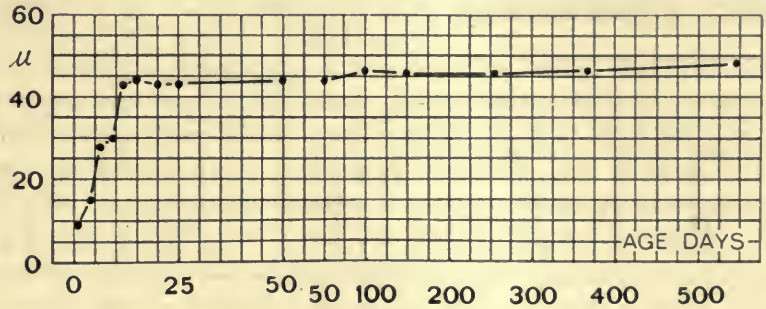

Chart 12 The radial basal breadth of the outer pillar cell, table 32, figure 2, distance 9.

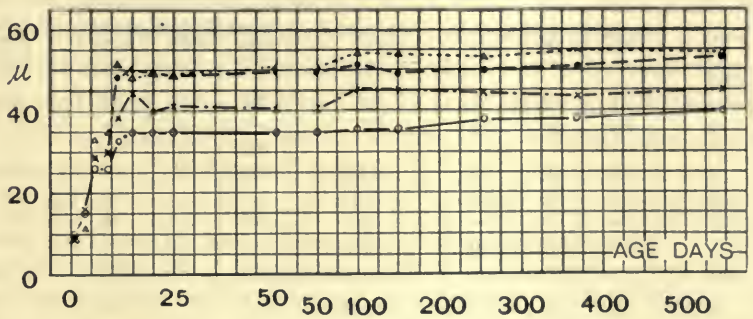

Chart 13 The radial basal breadth of the outer pillar cell, according to the turns of the cochlea, table 32, figure 2, distance 9.

derived from tables 22, 28, and 29. At the foot of the last column are given the ratios from 1 to 546, 9 to 546, 12 to 546, and 20 to 546 days. The values increase rapidly during the earlier stage, but after twelve days very slowly, as the ratios show.

The breadth is, at birth, largest in the basal and smallest in the apical turn. Very soon, however (six days), the reverse

relation appears, and the breadth increases from the base to turn III relatively rapidly, but from turn III to IV slowly. In table 33 the ratios are given in a condensed form. The radial breadth of the outer pillar cells as given by Retzius ('84) are as follows (table 34.)

TABLE 33—*Condensed*

Ratios of the radial basal breadth of the outer pillar cells—on age—according to turns of cochlea

AGE	BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 0.9	1 : 0.8	1 : 0.8
8	11	: 1.1	: 1.2	: 1.3
18	21	: 1.2	: 1.4	: 1.4
213	138	: 1.2	: 1.4	: 1.4

TABLE 34

Radial basal breadth of the outer pillar cells in μ (Retzius)

AGE	RABBIT				CAT			
	Basal turn	Middle turn	Apical turn	Average turn	Basal turn	Middle turn	Apical turn	Average turn
days								
New-born	21	22	23	22	36	30	30	32
3	30	40	30	33	—	—	—	—
3	—	—	—	—	36	30	—	—
7	65	66	60	64	36	54	36	42
10	52	60	69	60	—	—	—	—
11	—	—	—	—	50	60	18	43
14	57	80	80	72	—	—	—	—
30	—	—	—	—	—	60	60	—

This table shows that the breadth of the outer pillar cell increases in the rabbit and the cat continuously from birth to old age, as I have found in the rat. Also the value is generally smallest in the base, largest in the apex. though there are some exceptions. The main differences between the results of Retzius and mine is that the values in the rabbit are larger than in the rat. This is probably due to the differences in the size of the animals.

6. The radial distance between the habenula perforata and the outer border of the foot of the outer pillar cell. The determination of this distance is deemed necessary not only as a datum on growth in general, but also for its bearing on the difficult question of the shifting of the outer pillar cell, to be discussed later. On the other hand, this distance is identical with the radial length of the zona arcuata of the membrana basilaris (table 7. inner zone).

In table 35 (chart 14) are given the values for the radial distance between the habenula perforata and the outer corner of the outer pillar cell at base. At the foot of each column are given the ratios at 1 to 12, 1 to 20, 1 to 546, and 20 to 546 days. As table 35 shows, the distance increases continuously from birth to old age, rapidly up to twelve days, but later gradually. Up to three days the distance is slightly larger in the lower turns, but after this age the relation is reversed, and this persists through life.

The increasing ratio of the distance for each turn according to age is smallest in turn I and largest in turn IV. The ratios for the condensed data are given in table 36. While the ratio at birth is the same in each turn, 1:1.0, that of turn I to II is smallest for every condensed age. Also it is to be seen that the increase of the ratio in turn I to II is smallest and that in turns I to IV is largest. In Retzius' work ('84) we find the following values for this distance (table 37).

Table 37 shows that in the rabbit the growth changes are similar to those in the rat, though the absolute values are somewhat larger. As in preceding determinations, the values for the cat do not stand in the same relation as those for the rabbit, but indicate precocity. Some corresponding observations by Hensen, Böttcher, and others will be presented later.

7. The greatest height of the greater epithelial ridge (der grosse Epithelwulst (Bottcher) s. Organon Kollikeri) resp. of the inner supporting cells (fig. 4, G). The so-called greater epithelial ridge is a prominence formed by high cylindrical pseudostratified cells. It is situated axialward on the tympanic wall and continued outward to the lesser epithelial ridge. About the fate of this ridge there were various divergent opinions among the older

authors. Now, the view of Böttcher ('69) is generally accepted. This large prominence vanishes during development, and instead of it a deep and wide furrow lined with low epithelium appears. These epithelial cells become peripherally higher and finally lean

TABLE 35

Radial distance between habenula perforata and the outer corner of the outer pillar cells at base—on age (chart 14). For the average values see the third column in table 9

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	50	50	48	48	49
3	8	63	65	64	58	63
6	11	64	73	86	86	77
9	10	70	76	86	86	80
12	13	69	83	98	100	88
15	13	70	84	98	95	87
20	29	71	81	96	98	87
25	36	71	86	95	97	87
50	59	69	83	96	102	88
100	112	73	88	101	106	92
150	183	73	89	98	107	92
257	137	76	87	98	107	92
366	181	76	89	100	107	93
546	255	78	89	104	106	94
Ratios 1— 12 days		1 : 1.4	1 : 1.7	1 : 2.0	1 : 2.1	1 : 1.8
1— 20 "		: 1.4	: 1.6	: 2.0	: 2.0	: 1.8
1—546 "		: 1.6	: 1.8	: 2.2	: 2.2	: 1.9
20—546 "		: 1.1	: 1.1	: 1.1	: 1.1	: 1.1

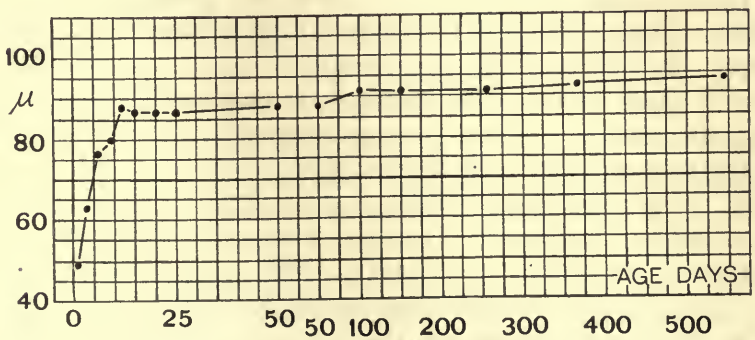

Chart 14 The radial distance between the habenula perforata and the outer corner of the outer pillar cell at base, table 35, figure 2, distance 5.

on the inner supporting cells, which are termed 'Grenzzellen' by Held ('02). The latter belong, of course, to this ridge, since the inner hair cell marks the outmost row in the ridge. The 'Grenzzellen' of Held, however, are different from other high cylindrical cells in the ridge, as they have a very intimate relation with the 'Phalangenzellen' of Held, stand with their bases just

TABLE 36—*Condensed*

Ratios of the radial distance between the habenula perforata and the outer corner of the outer pillar cells at base—on age

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.0	1 : 1.0
8	11	: 1.1	: 1.3	: 1.2
18	21	: 1.2	: 1.4	: 1.4
213	138	: 1.2	: 1.3	: 1.4

TABLE 37

Radial distance between habenula perforata and the outer corner of the outer pillar cells at base—in μ (Retzius)

Age	RABBIT				CAT			
	Basal turn	Middle turn	Apical turn	Average turn	Basal turn	Middle turn	Apical turn	Average turn
days								
New-born	75	80	75	77	105	105	120	110
2	80	90	100	90	—	—	—	—
3	—	—	—	—	80	120	—	—
7	100	115	107	107	78	110	120	103
10	100	120	129	116	—	—	—	—
11	—	—	—	—	120	129	108	119
14	106	140	129	125	—	—	—	—
30	—	—	—	—	85	120	120	108

outward from the habenula perforata and serve to support the inner hair cell as Deiters' cells support the outer hair cells.

Thus the greater ridge includes in its prominence three kinds of cells, the high cylindrical cells, the 'Grenzzellen' of Held and the inner hair cell.

The greatest height of this ridge is not situated at a fixed point, but first lies somewhat outward from the middle part and

after the furrow appears, passes outward towards the inner supporting cells. Thus the greater ridge decreases in thickness from birth to nine days of age, then increases gradually to twenty days. After twenty-five days the values diminish again very slowly but continuously.

In table 38 (charts 15 and 16) are given the values of the greatest height of the greater epithelial ridge from the basilar membrane

TABLE 38

Greatest height of the greater epithelial ridge (resp. of the inner supporting cells) on age (charts 15 and 16)

Age	Body weight	TURNS OF COCHLEA— μ				
		I	II	III	IV	Average height
days	*grams*					
1	5	68	65	66	63	66
3	8	49	49	56	57	53
6	11	40	40	41	40	40
9	10	36	40	41	42	40
12	13	38	41	48	53	45
15	13	44	46	52	58	50
20	29	50	53	63	66	58
25	36	51	51	63	63	57
50	59	50	50	59	63	56
100	112	48	49	59	63	55
150	183	47	49	56	61	53
257	137	47	51	56	62	54
366	181	46	49	57	60	54
546	255	44	50	56	60	53

Ratios 1— 9 days	1 : 0.6
12— 20 "	: 1.3
12—546 "	: 1.2
20—546 "	: 0.9
1—546 "	: 0.8

through the summit of the supporting cells, according to age. At the bottom of the last column is given the ratio at 1 to 9, 1 to 546, 12 to 20, 12 to 546, and 20 to 546 days of age.

The values in turn I are at birth the largest, but at three days the relation is reversed and remains so in the later age groups. Table 39 shows this relation from the condensed data.

Retzius ('84) gives in the rabbit and cat the following values (table 40).

In the rabbit the values decrease from birth till ten days, then increase; therefore, they agree in general with my results

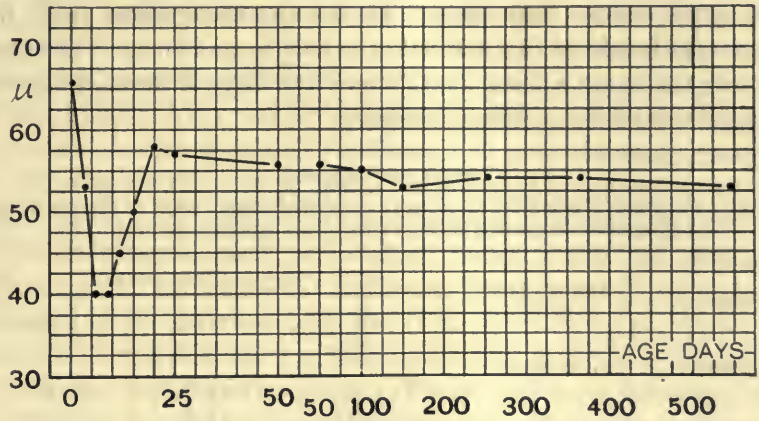

Chart 15 The greatest height of the greater epithelial ridge (resp. of the inner supporting cells) table 38, figures 4 to 12.

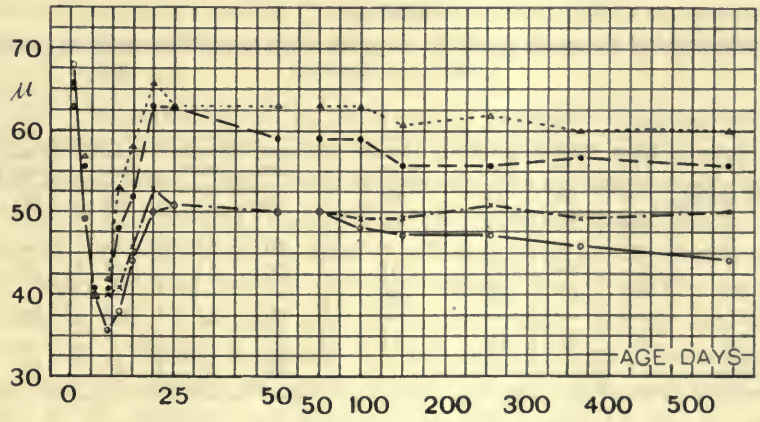

Chart 16 The greatest height of the greater epithelial ridge (resp. of the inner supporting cells) arranged according to the turns of the cochlea, table 38, figures 4 to 12.

on the rat, while in the cat they diminish from birth till thirty days though irregularly.

The absolute values are greater for the rabbit than for the rat during the earlier stage, but afterwards they are similar.

In the cat the early data give values similar to those for the rat, but the later values are lower.

Böttcher's observations ('69) on the cat, calf, and sheep also give larger values than mine. In the cat the greater ridge has an average height of 75 μ and in both the others of 90 μ. Therefore, even in the same animal (cat) there are large differences in the data presented by different authors.

TABLE 39—*Condensed*

Ratois of the greatest height of the greater epithelial ridge (resp. of the inner supporting cells) according to the turns of the cochlea—on age

Average age	Average body weight	RATIOS BETWEEB TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.0	1 : 0.9
8	11	: 1.0	: 1.1	: 1.2
18	21	: 1.1	: 1.2	: 1.3
213	138	: 1.0	: 1.2	: 1.3

TABLE 40

Greatest height of the greater epithelial ridge measured through the inner supporting cells, in μ (Retzius)

	RABBIT				CAT			
Age days	Basal turn	Middle turn	Apical turn	Average turn	Basal turn	Middle turn	Apical turn	Average turn
New-born	78	99	90	89	45	75	68	63
2	60	90	90	80	—	—	—	—
3	—	—	—	—	40	84	—	—
7	51	68	63	61	40	54	63	52
10	36	54	56	49	—	—	—	—
11	—	—	—	—	50	58	66	58
14	51	51	51	51	—	—	—	—
30	—	—	—	—	30	45	45	40

Gottstein ('72) thinks that the greater epithelial ridge does not diminish its height for some time after birth, but through the outward development of the labium tympanicum, and in addition to this through the growth of the labium vestibulare, the sulcus spiralis internus arises. He does not give measurements.

His idea was strongly opposed by Böttcher ('72) and my results are also opposed to Gottstein's view.

8. The radial distance between the labium vestibulare and the habenula perforata. The purpose of this measurement is to determine how the habenula perforata stands in relation to its surroundings during the development of the cochlea. The measurements of this distance is difficult. During the earlier stages, the labium vestibulare is quite undeveloped, especially in the upper turns. At birth we see on the inner surface of the greater epithelial ridge a small prominence under which the epithelial cells are short and pressed together so that the nuclei seem to be arranged in several rows (fig. 4). This appearance is due to the invasion of the subjacent connective tissue into the epithelium.

Thus the vestibular lip arises. We do not see a furrow at this time and cannot use the top of the furrow as a point for measuring as did Hensen ('63) in the ox and Böttcher ('69); in the embryo cat). To the measure the distance between the insertion of Reissner's membrane and the habenula perforata has no meaning for my purpose, because the length of the limbus laminae spiralis changes with age.

Thus I have measured the distance between the small epithelial prominence on the axial side of the greater ridge, corresponding to the edge of the labium vestibulare, and the habenula perforata.

In table 41 (charts 17 and 18) are given the values of the radial distance between the labium vestibulare and the habenula perforata. At the foot of the last column are given the ratios from 1 to 546, 9 to 546, and 20 to 546 days. As we see, the values are a little bit smaller at the earlier stage. After nine days they are almost the same in every stage. The small differences at the earlier and later stages are probably due to the retarded development of the labium vestibulare.

When we consider the values for this distance in each turn, it is evident that these increase from base to apex. In the condensed table 42 this relation is shown.

Hensen ('63) finds that the distance from the top of the furrow to the habenula perforata is in the fetal calf and in the ox the

same, 255 μ. He considers the holes of the habenula as a 'punctum fixum.' Böttcher ('69, '72) agrees with Hensen and gets in the cat embryo and the adult cat the following values (table 43).

TABLE 41

Radial distance between the labium vestibulare and the habenula perforata—on age (charts 17 and 18)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	100	108	120	130	115
3	8	80	110	130	137	114
6	11	82	105	135	137	115
9	10	83	108	137	145	118
12	13	80	102	139	148	117
15	13	82	107	144	157	122
20	29	84	106	146	153	122
25	36	82	105	147	150	121
50	59	82	104	137	147	118
100	112	80	103	151	154	122
150	183	80	107	141	144	118
257	137	83	105	143	150	120
366	181	79	105	135	149	117
546	255	79	105	143	150	119

Ratios 1—546 days	1 : 1.0
9—546 "	: 1.0
20—546 "	: 1.0

TABLE 42—*Condensed*

Ratios of the radial distance between the labium vestibulare and the habenula perforata according to turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.1	1 : 1.2	1 : 1.3
5	10	: 1.3	: 1.6	: 1.8
141	93	: 1.3	: 1.7	: 1.8

Comparing the results of both Hensen and Böttcher with my own, the values obtained by Hensen are large, as would be expected in the larger animal. The cat and rat however, give similar values. We conclude, therefore, that broadly speak-

ing, the habenula perforata is to be considered as a 'punctum fixum,' at least after birth.

9. The radial distance between the labium vestibulare and the inner edge of the head of the inner pillar cell. To measure the

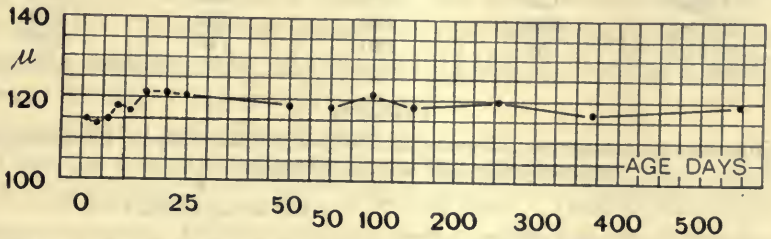

Chart 17 The radial distance between labium vestibulare and the habenula perforata, table 41, figure 10.

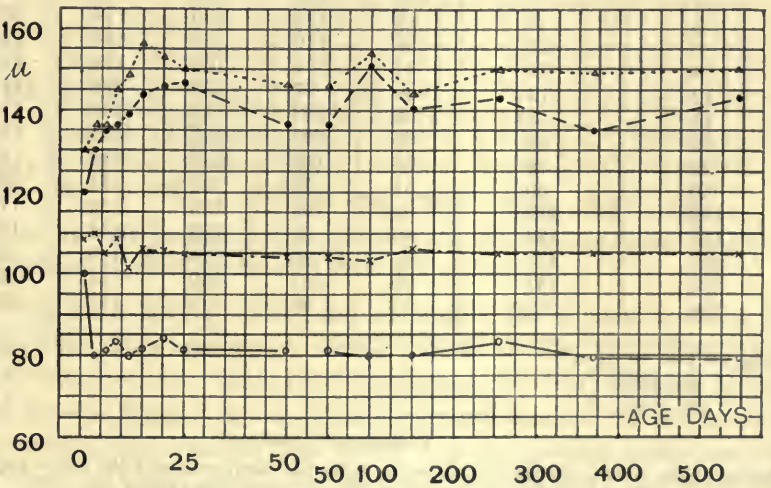

Chart 18 The radial distance between labium vestibulare and the habenula perforata according to the turns of the cochlea, table 41.

radial breadth from the labium vestibulare to the inner edge of the head of the inner pillar cell, I have used, at earlier stages, as in the preceding chapter, the same small prominence as an inner fixed point (fig. 4). In table 44 (chart 19) are given the values for this radial distance according to age. At the bottom of the last column are given the ratios from 1 to 9, 1 to 546

TABLE 43

Distance between labium vestibulare and habenula perforata in μ (Böttcher)

PLACE OF MEASUREMENT	CAT EMBRYO 9 CM. LONG	CAT EMBRYO 11.5 CM. LONG	CAT THREE DAYS OLD	ADULT CAT
I turn	120	120	120	100
II turn	130	130	130	110
III turn	150	140	140	130

TABLE 44

Radial distance between the labium vestibulare and the inner edge of the head of the inner pillar cell—on age (chart 19)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	111	126	138	130	126
3	8	84	118	150	170	131
6	11	88	119	159	180	136
9	10	94	131	168	179	143
12	13	69	97	138	156	115
15	13	66	103	137	149	114
20	29	66	103	137	148	114
25	36	65	100	136	148	112
50	59	61	98	129	144	108
100	112	64	99	139	153	114
150	183	60	99	129	143	108
257	137	67	100	134	149	113
366	181	60	102	130	151	111
546	255	55	99	128	143	106

Ratios 1— 9 days	1 : 1.1
1—546 "	: 0.8
12—546 "	: 0.9

TABLE 45—*Condensed*

Ratios of the radial distance between the habenula perforata and the inner edge of the head of the inner pillar cell according to the turns of the cochlea—on age

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.1	1 : 1.2	1 : 1.2
6	10	: 1.4	: 1.8	: 2.0
154	102	: 1.5	: 2.1	: 2.3

and 12 to 546 days of age. As the table shows, the values increase in general from birth to nine days; therefore, the surface of the greater epithelial thickening from the labium vestibulare to its outer boundary becomes, during the earlier stage, wider and wider, then decreases sharply, and after that continuously but slowly. This sudden diminishing of the distance has a very intimate relation with the change in the form of the papilla spiralis at this stage of development.

This point I will discuss later.

That the values increase from the base to the apex first rapidly and later less rapidly, is also to be seen here. Table 45 shows this relation clearly. It is remarkable, however, that the ratio becomes

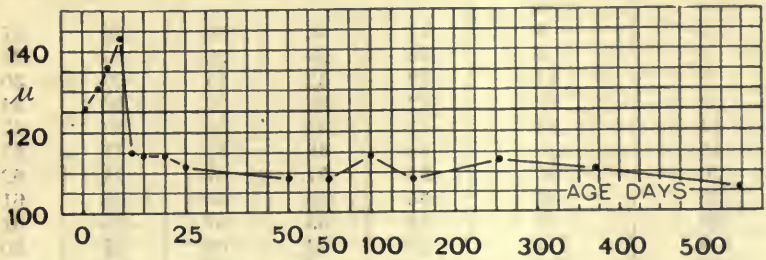

Chart 19 The radial distance between the labium vestibulare and the inner edge of the head of the inner pillar cell, table 44.

at each turn larger with age, although the absolute value is after nine days generally smaller than at the preceding age. Therefore, we see that the diminution of the distance after nine days is largest in the basal turn and smallest in the apical.

Hensen ('63) asserts that there is a movement axialward of the organ of Corti (resp. the head of the pillar cell), but gives no measurements. Neither Böttcher nor Retzius measured this distance. Prentiss ('13, page 445) states that "the distance between the inner angle of the cochlea and the pillar cells, two definite points, may be measured with considerable accuracy and shows no important change in the position of the spiral organ from the 13 cm. to the 18.5 cm. stage, nor later in the new born animal" (pig). But he also does not record his measurements.

Hardesty ('15, p. 54) says "that the space occupied by the width of the greater epithelial ridge increases throughout the coils of the cochlea up to pigs of 15 to 16 cm., and thereafter it begins to decrease very perceptibly." He measured the width "from the membrana propria of the epithelium of the greater ridge, at its most axial extension under Huschke's teeth, to the apical end of the inner hair cell of the spiral organ." The

TABLE 46

Vertical distance from the membrana basilaris to the surface of the pillar cells—on age (chart 20)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	35	36	39	36	37
3	8	30	29	29	29	29
6	11	29	32	31	29	30
9	10	32	33	35	36	34
12	13	41	45	50	52	47
15	13	44	48	53	57	51
20	29	53	57	67	71	62
25	36	55	56	66	68	61
50	59	53	55	67	68	61
100	112	53	54	64	67	60
150	183	52	54	63	66	59
257	137	53	56	63	69	60
366	181	51	56	66	67	60
546	255	52	55	62	66	59

Ratios 1— 12 days	1 : 1.3
1— 20 "	: 1.7
1—546 "	: 1.6
12—546 "	: 1 3
20—546 "	: 1.0

method of measurement differs from mine, so the results cannot be compared directly. While the distance in the rat increases to nine days of age, that in the pig decreases perceptibly in fetuses more than 16 cm. long.

According to Hardesty ('15, p. 55). "the decrease in the I and III half turns may be as much as one-third of the width of the greater ridge when at its maximum size and activity." And "after the tectorial membrane is about completely produced,

and while the spiral organ is enlarging, the inner hair cells, and therefore the organ, may be moved in the apical coil of the cochlea axialward a distance of about half the maximum width of the greater epithelial ridge,....."

The differences of the values in the rat at 9 and 546 days are in the basal and apical turn about the same, 39 and 36 μ, respectively (table 44). Thus while the inner edge of the inner pillar cell approaches at 546 days in the basal turn by as much as 41 per cent of the distance present at nine days, that in the

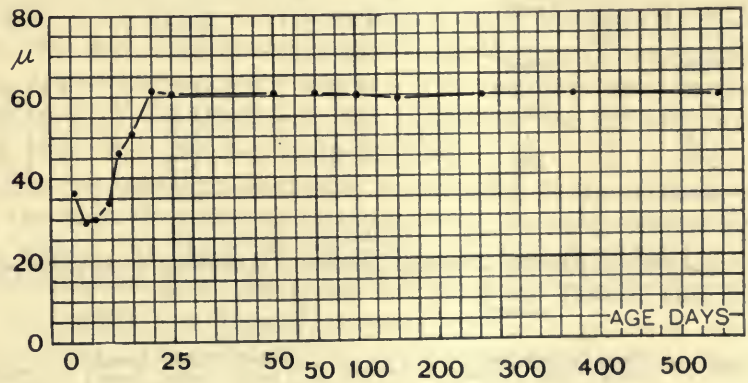

Chart 20 The vertical distance from the membrana basilaris to the surface of the pillar cells, table 46, figure 1, *1–1*.

apex moves only 20 per cent inward in old age. This result is the reverse of that obtained in the pig by Hardesty. The reason for this contradiction I will discuss later.

10. The vertical distance from the membrane basilaris to the summit of the pillar cells. The method of getting the vertical distance from the membrana basilaris to the surface of the pillar cells is shown in figure 1, line 1–1. In table 46 (chart 20) are given the values thus obtained. At the foot of the last column are given the ratios of this distance at 1 to 12, 1 to 20, 1 to 546, 12 to 546, and 20 to 546 days. The average value is relatively large at birth, it diminishes at three days, then increases more rapidly to twenty days. After this it decreases very slowly. The maximum height of the arch of Corti is at twenty days of

age. Comparing the values for the height in each turn, we find that from nine days they increase from the basal to the apical turn. This relation can be easily seen in table 47.

Retzius ('84) gives in the rabbit and cat the following values (table 48).

TABLE 47—*Condensed*

Ratios of the vertical distance from the membrana basilaris to the surface of the pillar cells—according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.1	1 : 1.0
1	11	: 1.1	: 1.1	: 1.1
18	21	: 1.1	: 1.2	: 1.3
213	138	: 1.0	: 1.2	: 1.3

TABLE 48

Vertical distance from the membrana basilaris to the summit of the pillar cells

	RABBIT				CAT			
Age	Basal turn	Middle turn	Apical turn	Average	Basal turn	Middle turn	Apical turn	Average
days								
New-born	45	70	61	59	45	60	48	51
2	45	69	40	51	—	—	—	—
3	—	—	—	—	39	60	—	—
7	46	60	60	55	45	47	50	44
10	45	69	69	61	—	—	—	—
11	—	—	—	—	50	60	42	51
14	45	57	66	56	—	—	—	—
30	—	—	—	—	33	51	57	47

Table 48 shows that the height of the arch of Corti in the rabbit approximates that in the rat, though there are considerable differences in the earlier stages. In the former the arch of Corti develops after birth only a little, and is therefore more precocious than in the rat. In the cat the same relation is to be seen, but the absolute values in the latter animal are smaller than in either the rabbit or the rat.

11. The greatest height of the tunnel of Corti. Some authors have reported in several animals the appearance of the tunnel of Corti just after birth, or even in later intrauterine life. In the rat, however, it first appears through all the turns after the ninth day. Sometimes we see it at nine days in the lower turn, though not yet in the upper. The method of measuring the height is shown in figure 1, line *1–1′*. Table 49 (charts 21 and 22) gives the values for the greatest height of the tunnel of Corti. At the foot of the last column are given the ratios from 12 to 25, 12 to 546, and 25 to 546 days.

As the table shows, the space appears in all the turns at twelve days and has considerable height. This increases to twenty-five days, than decreases very slowly. This increase and decrease correspond to the changes in the distance of the summit of the pillar cells from the basilar membrane.

When we consider the height in each coil of the cochlea, we find the value increases from the base to the apex, first rapidly then slowly. In table 50 this relation is clearly shown.

Retzius ('84) gives the values for the adult rabbit, man and cat (one month) as follows (table 51).

According to this table, the average height is in the adult man, cat, and rabbit somewhat less than in the rat.

12. The height of the papilla spiralis at the third series of the outer hair cells. The measurements were taken along the line *2–2* shown in figure 1. The growth of this vertical height depends not only upon the increase of the length of the corresponding outer hair cell, but chiefly upon the development of the Deiters' cells, especially of the outermost row, and of the sustentacular cells of Hensen.

In table 52 (charts 23 and 24) are given the values for this vertical height of the papilla spiralis at the third series of the outer hair cells according to age. At the bottom of the last column are the ratios at 1 to 12, 1 to 20, 1 to 546, and 20 to 546 days. The heights decrease at three days, but increase from nine to twelve days very rapidly, nearly doubling their minimal values, and reach a maximum at twenty days. After that time they decrease very gradually to the end of the record. There-

TABLE 49

Greatest height of the tunnel of Corti—on age (charts 21 and 22)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	—	—	—	—	—
3	8	—	—	—	—	—
6	11	—	—	—	—	—
9[1]	10	—	—	—	—	—
12	13	29	33	39	37	35
15	13	31	34	42	46	38
20	29	37	42	52	56	47
25	36	39	41	54	56	48
50	59	38	41	53	57	47
100	112	38	43	51	56	47
150	183	37	41	49	54	45
257	137	38	43	51	56	47
366	181	37	41	52	53	46
546	255	36	39	48	53	44

Ratios 12— 25 days	1 : 1.4
12—546 "	: 1.3
25—546 "	: 0.9

[1] In one case—nine days old—which could hear the space was found through all the turns of the cochlea.

TABLE 50—*Condensed*

Ratios of the greatest height of the tunnel of Corti—according to the turns of the cochlea—on age

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
12	13	1 : 1.1	1 : 1.3	1 : 1.3
18	21	:1.1	: 1.4	: 1.5
213	138	: 1.1	: 1.3	: 1.4

TABLE 51

The greatest height of the tunnel of Corti—in μ (Retzius)

RABBIT				CAT (one month)				MAN			
Basal	Middle	Apical	Aver-age	Basal	Middle	Apical	Aver-age	Basal	Middle	Apical	Aver-age
30	39	36	35	18	37	36	30	28	45	49	41

fore, the difference between the ratios at 1 to 20 and 1 to 546 days is very small.

At twelve days and after, the values for the height increase in passing from the base to the apex, at first rapidly, then more slowly. In the earlier stages this relation is obscure or reversed.

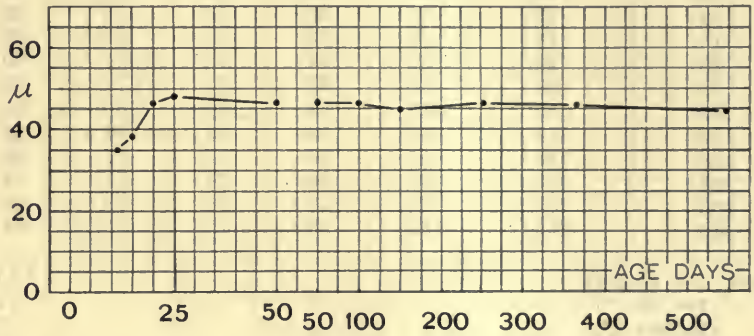

Chart 21 The greatest height of the tunnel of Corti, table 49, figure 1, *1–1'*.

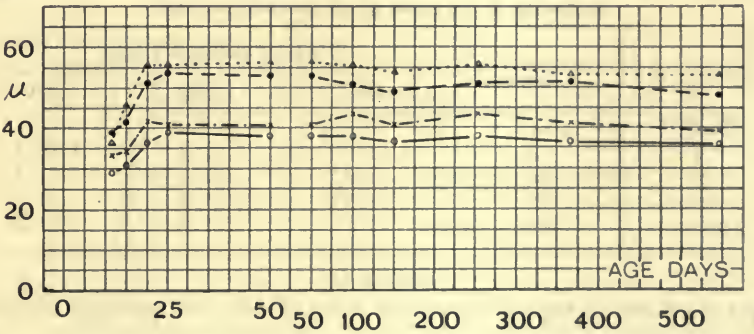

Chart 22 The greatest height of the tunnel of Corti, according to the turns of the cochlea, table 49.

In the condensed table 53 are given the ratios in each turn. While the ratio of each turn before eight days is about 1:1.1, and between turns I and II remains constant in the later age, that for I to III and I to IV is at 18 and 213 days decidedly larger. Therefore, the increase of the height is most marked in the III and IV turn, as shown in chart 24.

TABLE 52

Height of the papilla spiralis at the third series of outer hair cells—on age (charts 23 and 24)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	35	35	39	28	34
3	8	22	23	25	26	24
6	11	25	24	25	23	24
9	10	28	28	27	28	28
12	13	40	49	54	56	50
15	13	46	53	65	66	58
20	29	56	61	76	81	69
25	36	56	61	76	78	68
50	59	53	59	78	80	68
100	112	54	59	74	79	67
150	183	55	57	75	77	66
257	137	54	59	74	81	67
366	181	52	58	75	78	66
546	255	52	58	72	75	64

Ratios	1— 12 days	1 : 1.5
	1— 20 "	: 2.0
	1—546 "	: 1.9
	20—546 "	: 0.9

TABLE 53—*Condensed*

Ratios of the height of the papilla spiralis at the third series of outer hair cells—according to the turns of the cochlea—on age

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.1	1 : 0.8
8	11	: 1.1	: 1.1	: 1.1
18	21	: 1.1	: 1.4	: 1.5
213	138	: 1.1	: 1.4	: 1.5

TABLE 54

Height of the papilla spiralis at the third series of outer hair cells in μ (Retzius)

AGE	RABBIT				CAT			
	Basal turn	Middle turn	Apical turn	Average	Basal turn	Middle turn	Apical turn	Average
days								
New-born	48	70	60	59	45	60	45	50
2	45	70	54	56	—	—	—	—
3	—	—	—	—	40	58	—	—
7	54	69	66	63	42	53	48	49
10	42	86	84	71	—	—	—	—
11	—	—	—	—	60	72	42	58
14	60	87	90	79	—	—	—	—
30	—	—	—	—	36	57	70	54

Retzius ('84) finds in the rabbit and cat the values for this height given in (table 54).

Comparing these average numbers with mine, it appears that the height in the rabbit is greater, and in the cat smaller than

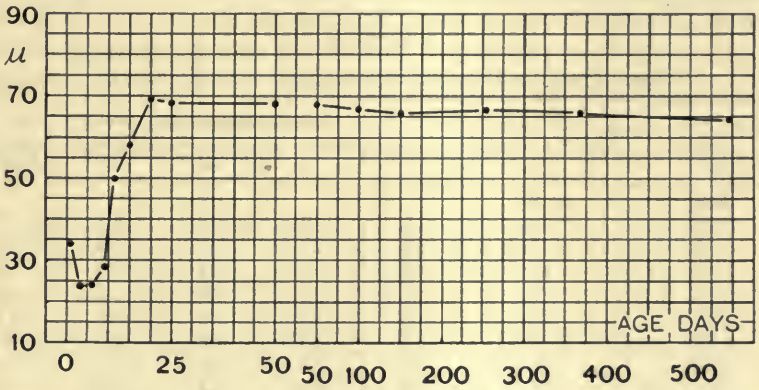

Chart 23 The height of the papilla spiralis at the third series of the outer hair cells, table 52, figure 1, *2–2*.

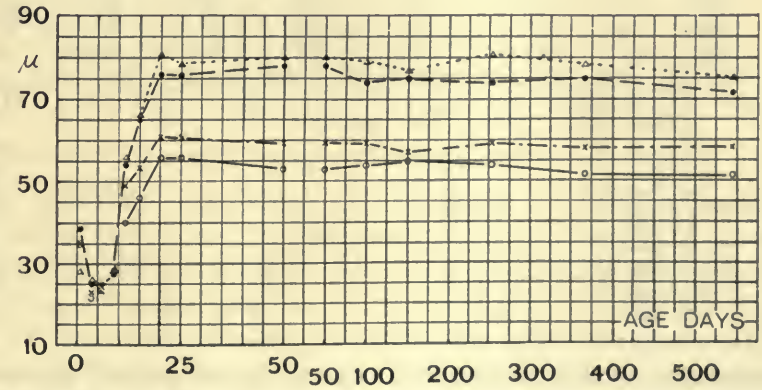

Chart 24 The height of the papilla spiralis at the third series of the outer hair cells, according to the turns of the cochlea, table 52.

in the rat. In both animals the values increase rapidly at ten to eleven days of age, as in the albino rat, but the height in these animals is at the earlier stage almost twice as large as in the rat. Hardesty ('15) measured the thickness of the organ of Corti in

the pig in a somewhat different way, using the vertical line from the basilar membrane proper through the middle of the outer hair cell to the surface of the organ, and found the increase in thickness to take place most rapidly at the stages before full term, though it seems to continue after birth. I have not made cor-

TABLE 55

Greatest height of Hensen's supporting cells—on age (chart 25)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ				
		I	II	III	IV	Average
days	*grams*					
1	5	36	36	38	31	35
3	8	18	21	21	24	21
6	11	21	20	21	18	20
9	10	20	23	23	24	23
12	13	40	49	56	58	51
15	13	44	56	69	72	60
20	29	64	64	86	87	75
25	36	69	71	84	86	78
50	59	71	74	87	89	81
100	112	77	78	87	89	83
150	183	76	77	93	93	85
257	137	81	83	89	89	86
366	181	82	83	89	91	86
546	255	79	79	92	93	86

Ratios 1— 6 days	1 : 0.6
1— 12 "	: 1.5
1— 20 "	: 2.1
1—546 "	: 2.5
6— 12 "	: 2.6
6— 20 "	: 3.8
6—546 "	: 4.3
12— 20 "	: 1.5
12—546 "	: 1.7
20—546 "	: 1.1

responding studies on the rat. In the latter animal, however, the rapid increase usually appears at twelve days of age, when the animal as a rule first responds to auditory stimuli, and thus we have a correlation between the development of the organ and the beginning of the function, which will be discussed later. In the case of one rat that could hear at nine days this change had already occurred.

13. The greatest height of Hensen's supporting cells. The older authors (Kölliker and others) thought that the arch of Corti marks the highest point of the papilla which slopes from this point gradually outward to the cells of the zona pectinata. Against this erroneous idea Hensen ('63) first published observations showing that the highest point is in the papilla which ascends laterally from the outer hair cells, and then slopes abruptly and passes over to the cells of the sulcus spiralis externus. We term this prominence Hensen's prominence and the cells, Hensen's supporting cells. The measurements of the height of

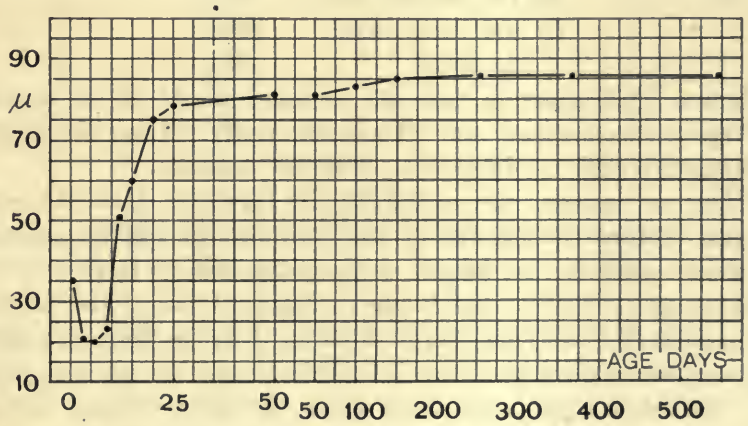

Chart 25 The greatest height of Hensen's supporting cells, table 55.

these cells were made along *3—3* in figure 1. Table 55 (chart 25) shows the values for the greatest vertical height of these supporting cells according to age. At the foot of the last column are given the ratios from 1 to 6, 1 to 12, 1 to 20, 1 to 546, 6 to 12, 6 to 20, 6 to 546, 12 to 20, 12 to 546, and 20 to 546 days. The values diminish at the earlier stage from birth to six or nine days.

At twelve days they increase suddenly, more than doubling. After that they increase to old age, rapidly up to twenty days and then slowly. Here also the height increases from the base to the apex, the most marked increase occurring between turns II and III. In table 56 this relation is clearly shown. Retzius ('84) gets values of this height in the rabbit and cat as follows (table 57).

In both the rabbit and the cat the height increases at ten to eleven days very considerably, as it does in the rat. Only there is a large difference in the absolute values for the three animals, these being largest in the rabbit and smallest in the cat. The final average values in the cat are nearly the same as those in the rat at the same age.

Kolmer ('07) finds in the calf the value in the highest point of the organ of Corti in the region of the innermost Hensen's cells as follows:

In the basal turn,	84 μ
In the second turn,	90 μ
In the third turn,	105 μ
Average,	93 μ

Hensen ('63) gives in man the average height of the papilla as 90 μ in the hamulus and 60 μ in the radix. Thus the height of Hensen's cells is different in different animals.

When we consider the growth in the height of Hensen's cells we can picture the change of the form in the papilla spiralis. As shown already, the height of the pillar cells is largest at the earlier stage, when the papilla has its highest point at the summit of the arch of Corti, and slopes downward to the Hensen's cells. But at twelve days the form is reversed, and the highest point is in Hensen's prominence from which the surface slopes inward more or less steeply to the surface of the pillar cells and the inner supporting cells. Thus the surface of the papilla does not run parallel to the basilar membrane, but makes with it a sharp angle opening outward. This angle has been measured.

14. The angle subtended by the extension of the surface of the lamina reticularis with the extended plane of the membrana basilaris. As just stated, the lamina reticularis after the earlier stages is not parallel to the membrana basilaris, but forms an angle with it. The measurements of this angle Θ, were taken as shown in lines *4–4′* in figure 1. In table 58 (chart 26) are given the values for the angle in degrees. Before nine days there is no appreciable angle. From twelve to twenty days the angle increases rather rapidly, and after twenty days continuously but slowly. The ratio at the bottom of the last column shows this clearly.

Comparing the values of the angle in each turn according to age, there is no clear evidence that it increases from base to apex, though it tends to be largest in turn III and next largest in turn II. The condensed table 59 shows these relations. Retzius ('84) finds this angle in the rabbit and cat to be as in table 60.

TABLE 56—*Condensed*

Ratios of the greatest height of Hensen's supporting cells according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN SUCCESSIVE TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.1	1 : 0.9
8	11	: 1.1	: 1.2	: 1.2
18	21	: 1.1	: 1.4	: 1.5
213	138	: 1.0	: 1.2	: 1.2

TABLE 57

Greatest height of Hensen's supporting cells in μ (Retzius)

	RABBIT				CAT			
Age Days	Basal turn	Middle	Apical	Average	Basal	Middle	Apical	Aver-age
New-born	38?	60?	50?	49?	45	50	39	45
2	55?	60?	—	—	—	—	—	—
3	—	—	—	—	39	54	—	—
7	48	81	67	65	57	50	40	49
10	105	125	105	112	—	—	—	—
11	—	—	—	—	75	78	45	66
14	—	150	120	—	—	—	—	—
30	—	—	—	—	50	69	95	71

Retzius also finds in man in the basal turn 25°, in the middle 35°, and in the apical 23°. Thus the angle always increases with age, but has different absolute values in different mammals and always tends to be greater in the middle turns.

15. Lengths of the inner and outer pillar cells. The measurements of length were taken as shown by lines *1–1*, and *2–2* as in figure 2. This does not give the total length, but the length from the base to the point, just below the joint. As is well

TABLE 58

Angle of the lamina reticularis with the plane of the membrana basilaris—in degrees, θ (chart 26)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA—DEGREES				
		I	II	III	IV	Average
days	*grams*					
1	5	—	—	—	—	—
3	8	—	—	—	—	—
6	11	—	—	—	—	—
9	10	—	—	—	—	—
12	13	7	12	13	9	10
15	13	11	14	13	13	13
20	29	15	13	11	11	13
25	36	14	14	13	13	14
50	59	15	15	17	11	15
100	112	15	14	16	14	15
150	183	15	15	19	17	17
257	137	13	15	18	17	16
366	181	16	15	16	16	16
546	255	16	16	17	17	17
Vertical averages		13.7	14.3	15.3	13.8	

Ratios 12— 20 days 1 : 1.3
12—546 " : 1.7

TABLE 59—*Condensed*

Ratios of the angle of the lamina reticularis with the plane of the membrana basilaris according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
12	13	1 : 1.7	1 : 1.9	1 : 1.3
18	21	: 1.0	: 0.9	: 0.9
213	138	: 1.0	: 1.2	: 1.0

TABLE 60

Angle of the lamina reticutaris with the plane of the membrana basilaris in degrees (Retzius)

	RABBIT				CAT			
Age	Basal turn	Middle turn	Apical turn	Average	Basal turn	Middle turn	Apical turn	Average
days								
New-born	0	—5?	—8?	—	0	—	—5? —8?	—
2	0	0	—	—	—	—	—	—
3	—	—	—	—	0	—5? —8?	—	—
7	17	19	—11	—	5	5	—10	—
10	20	30	23	24	—	—	—	—
11	—	—	—	—	20	10—20	0	—
14	25	50	45	40	—	—	—	—
30	—	—	—	—	18	23	20	20

known, the inner and outer pillar cells when mature show a more or less S-shaped curvature, though they are straighter in the earlier stages. Thus the length as measured in the adult cochlea is somewhat smaller than the natural lengths.

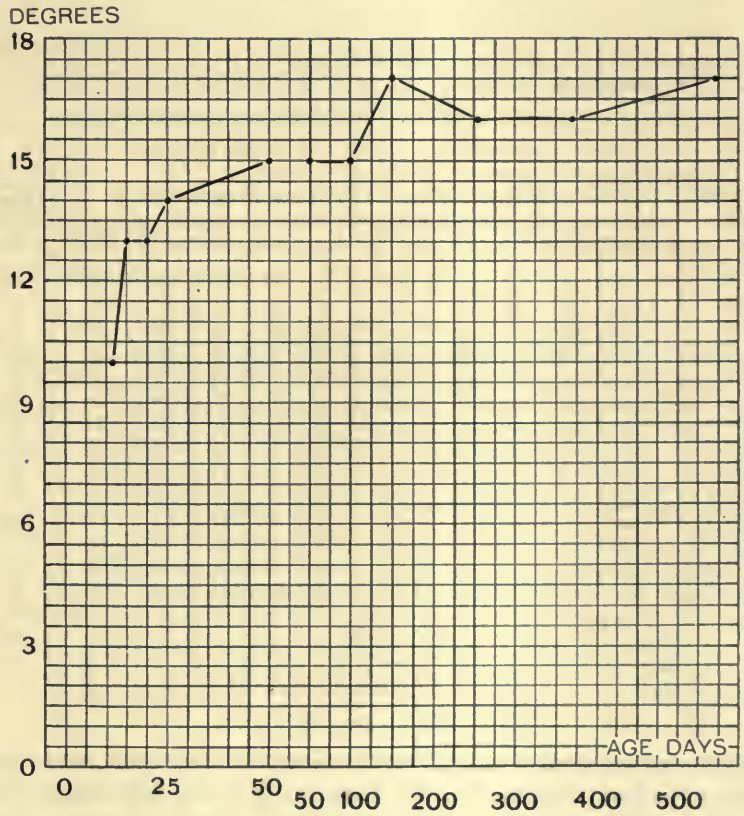

Chart 26 The angle subtended by the extension of the lamina reticularis with the extended plane of the membrana basilaris, in degrees, table 58, figure 1, 4–4′, θ.

In table 61 (charts 27 to 32) is given the values for the lengths of the inner and outer pillar cells according to age. At first we shall consider the average values for the length of the inner and outer pillar cells taken together. This length diminishes at three days. From three to twelve days it increases rapidly,

and from twelve to twenty days more slowly. After twenty days it decreases a little. The ratios at the bottom of the last column show these relations. The familiar fact, that the length increases from the base to the apex is clearly shown in chart 28.

TABLE 61

Lengths of the inner and outer pillar cells (without head) measured from the footplate on the membrana basilaris to the point directly below the junction (charts 27 to 32)

AGE	BODY WEIGHT	INNER PILLAR					OUTER PILLAR					Combined Average
		Turns of the cochlea μ					Turns of the cochlea μ					
		I	II	III	IV	Average	I	II	III	IV	Average	
days	*gms*											
1	5	28	29	29	29	29	24	27	27	26	26	28
3	8	26	23	26	23	25	19	20	20	21	20	23
6	11	35	36	36	37	36	21	26	27	26	25	31
9	10	35	39	41	40	39	26	26	29	29	28	34
12	13	33	38	44	44	40	46	59	72	72	62	51
15	13	34	38	48	51	43	44	59	74	78	64	54
20	29	43	47	56	60	52	56	65	79	83	71	62
25	36	43	47	56	60	52	53	64	80	84	70	61
50	59	42	44	55	61	51	52	64	79	84	70	61
100	112	42	44	53	58	49	52	62	79	84	69	59
150	183	41	43	54	59	49	51	64	76	85	69	59
257	137	40	44	53	60	49	53	64	75	85	69	59
366	181	39	45	53	59	48	50	64	78	83	69	59
546	255	41	44	53	58	49	49	64	78	83	69	59
Ratios	1– 12 days					1 : 1.4					1 : 2.4	1 : 1.8
	1– 20 "					: 1.8					: 2.7	: 2.2
	1–546 "					: 1.7					: 2.7	: 2.1
	20–546 "					: 0.9					: 1.0	: 1.0

When we calculate the average values of the inner and outer pillar cells from Retzius table ('84), we get the following (table 62).

TABLE 62

Combined lengths of the inner and outer pillars from the foot plate to a point directly below the junction—in μ (Retzius)

RABBIT (adult)				CAT (adult)				MAN (adult)			
Basal turn	Middle turn	Apical turn	Average turn	Basal turn	Middle turn	Apical turn	Average	Basal turn	Middle turn	Apical turn	Average
66	85	78	76	55	75	73	67	55	84	87	75

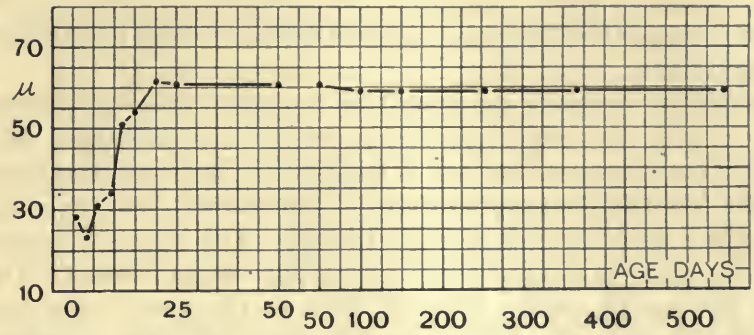

Chart 27 The length of inner and outer pillar cells combined, without head, measured from the foot plate on the membrana basilaris to the point directly below the junction, table 61, figure 2, *1–1*, *2–2*.

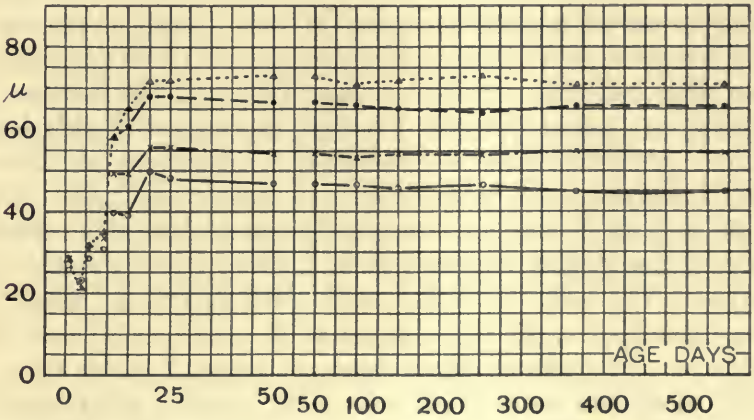

Chart 28 The length of inner and outer pillar cells combined, without head, measured from the foot plate on the membrana basilaris to the point directly below the junction, according to the turns of the cochlea, table 61.

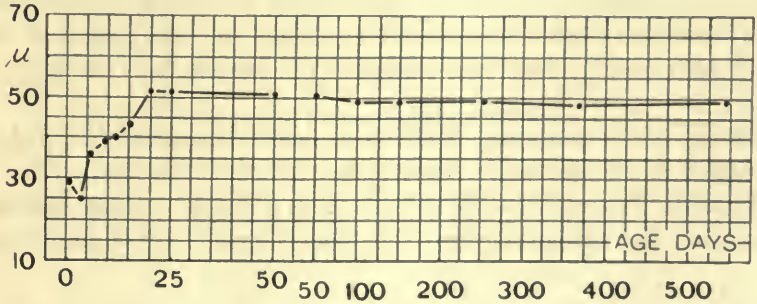

Chart 29 The length of inner pillar cell without head, table 61, figure 2, *1–1*.

As table 62 shows, the values in these mammals are larger than those in the albino rat—a result which fits with our previous observations.

When we consider the length of the inner pillar cells alone, we see that the values (chart 29) here also increases from three days to twenty days, but not so largely as in the combined values of the inner and outer pillar cells. After twenty days the values for the inner pillar cells decrease slightly. This relation is shown by the ratios at the bottom of the corresponding column. That the increase progresses from the base to the apex, being most marked in turn III, is illustrated in chart 30. The condensed table 63 shows those relations also. The one-day-old rat is an exception.

We turn now to the growth in the length of the outer pillar cells. As we see in table 61 (chart 31), the length of the outer pillar cell does not increase so much from one to nine days as the inner pillar cell did. At twelve days, however, the increase in length is very marked, that is, 2.2 times as much as at nine days.

After the outer pillar cell reaches its maximum at twenty days, it decreases only slightly with advancing age. The ratios at the bottom of the corresponding column show this relation clearly. The length increases from base to apex, though this relation is not well established until twelve days, as shown in table 61 and chart 32. The ratios of the outer pillar cells according to the turns of the cochlea are shown in table 64.

The inner and outer pillar cells show marked differences in their growth. While at the earlier ages the length of the inner is greater than that of the outer, yet after twelve days this relation is reversed. Moreover, from nine to twelve days the growth is gradual in the inner pillar cells, but rapid in the outer. The condensed table 65 shows the values for the length of the inner and outer pillar cells separately. In the last column are given the ratios between them.

In the accompanying table 66 I have compared the values obtained in the rat with those given by other authors.

As table 66 shows, the absolute values differ in various animals. However, the ratios between the values for the inner and outer

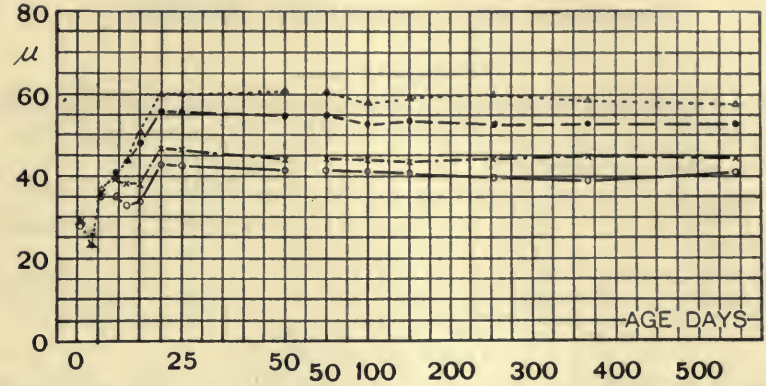

Chart 30 The length of the inner pillar cell without head, according to the turns of the cochlea, table 61.

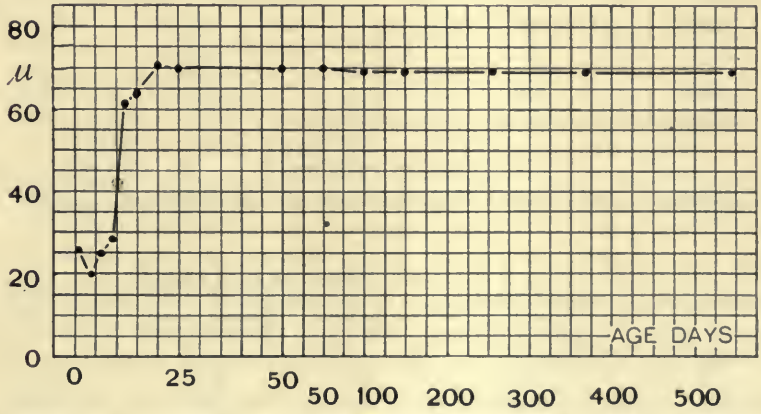

Chart 31 The length of outer pillar cells without head, table 61, figure 2, 2–2.

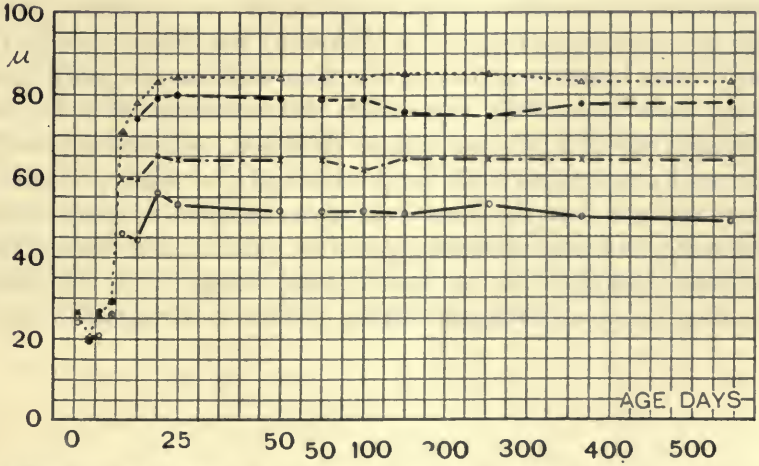

Chart 32 The length of outer pillar cells without head, according to the turns of the cochlea, table 61.

TABLE 63—*Condensed*

Ratios of the length of the inner pillar cells—according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.0	1 : 1.0
8	11	: 1.1	: 1.2	: 1.1
18	21	: 1.1	: 1.3	: 1.4
213	138	: 1.1	: 1.3	: 1.4

TABLE 64—*Condensed*

Ratios of the length of the outer pillar cells according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.1	1 : 1.1	1 : 1.0
8	11	: 1.2	: 1.3	: 1.3
18	21	: 1.2	: 1.5	: 1.6
213	138	: 1.3	: 1.5	: 1.6

TABLE 65—*Condensed*

Comparison of the average length of the inner and outer pillar-cells—without head.

AVERAGE AGE	AVERAGE BODY WEIGHT	AVERAGE LENGTH OF PILLAR CELLS WITHOUT HEAD		RATIOS OF INNER TO OUTER
		Inner	Outer	
days	*grams*			
1	5	29	26	1 : 1.0
8	11	35	34	: 1.0
18	21	48	68	: 1.4
213	138	50	69.	: 1.4

pillar cells are smallest in man and in the rat and alike in the other two forms, Retzius ('84). Hensen ('63) states that in the base of the human cochlea both pillar cells are equally long. Later, Pritchard ('78) supported this observation. In the literature, however, no one except these two authors report the inner and outer pillar cells in the base of the adult cochlea as equal in length, but the inner is always stated to be shorter than the outer. We may therefore say that most authors agree that the inner pillar cells are at earlier stages longer than the outer, then they become equal, and finally the outer surpass the inner.

TABLE 66

Lengths of inner and outer pillars in several mammals according to different authors. Measurements in μ

		INNER PILLAR					OUTER PILLAR					
Authors	Animals	Basal turn	Middle	Apical		Av.	B.	M.	A.		Av.	Ratio
Corti	Mammals	30	30	34		31	45–49	54–58	69		57	1 : 1.8
Hensen	Man	48	—	86 (Hamulus)		48	—		98 (Hamulus)			
Retzius	Rabbit	56	60	60		59	75	110	95		93	: 1.6
	Cat	41	54	57		51	68	95	89		84	: 1.6
	Man	48	68	70		62	62	100	103		88	: 1.4
Wada	Albino rat	I	II	III	IV		I	II	III	IV		
	after 20 days	41	45	54	59	50	52	64	78	84	70	: 1.4

16. Inner and outer hair cells. For a long time the inner and the outer hair cells have been regarded as the most important elements in the papilla spiralis. As these sense cells have a delicate histological structure which is readily altered, the systematic study of their growth, especially after the appearance of hearing, is a difficult matter. Though there are some observations on the length of these cells, detailed studies on their growth have not been made heretofore. I have therefore endeavored to follow the changes of their size during the postnatal period. It is first necessary to determine the form of these cells. They are generally described as cylindrical, but this description is inexact. Moreover, the inner and outer hair cells are somewhat different in shape. The former has on the surface a large oval terminal disk, which is wide in the spiral and narrow in the radial direction. This narrows downwards to a thinner neck which expands into the broader body and terminates in a more or less round but somewhat pointed irregular end.

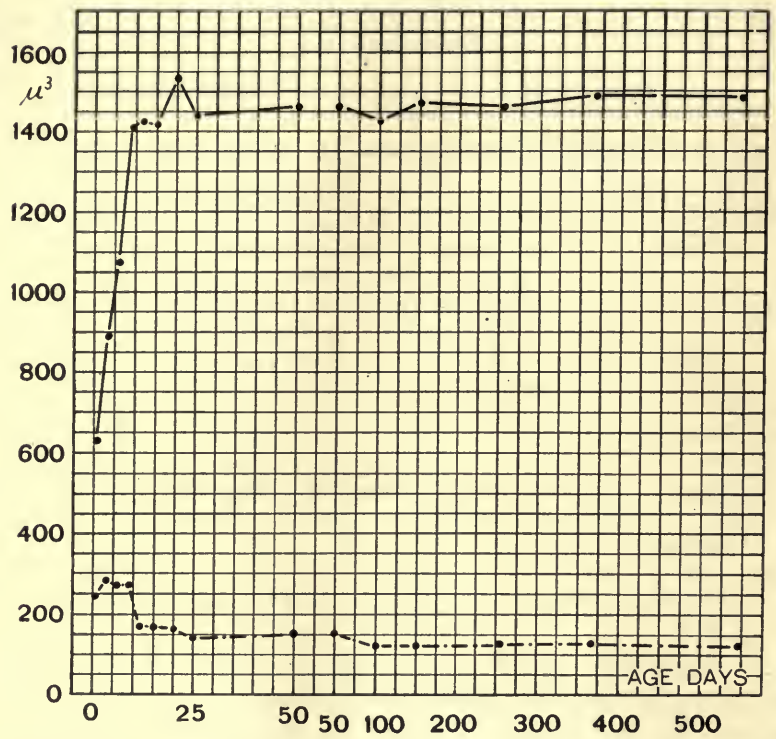

Chart 33 The weighted volume of inner and outer hair cells combined, and of their nuclei in cubic micra, tables 67 and 69.

———— Weighted volume of inner and outer hair cells combined.

–·–·–·–·– Weighted volume of nuclei of inner and outer hair cells combined.

The outer hair cells have a much more cylindrical form, their upper terminal disk is not so wide and not round, but hexagonal. They become a bit thin in the neck, then wide in the body. Their lower end is rounded. In order, however, to determine the cell volume, the cell form has been taken as that of a cylinder. For computation, the average of the diameters measured in three places, the end disk, neck, and cell body, was taken as the diameter and the length of the cell as the length of the cylinder. From these data the volume of the cylinder was computed.

In table 67 are given the values for the volume of the cell bodies in the (1) inner and (3) outer hair cells separately and the weighted volume of both cells (in the radial section of the rat cochlea we see one row of inner and three rows of outer hair cells), according to age.

TABLE 67

Average volumes of the inner and outer hair cells—in cubic micra (charts 33 to 37)

AGE	BODY WGHT	INNER HAIR CELL					OUTER HAIR CELL					WEIGHTD AVERAGE VOLUME
		Turns of the cochlea— μ^3					Turns of the cochlea— μ 3					
		I	II	III	IV	Average	I	II	III	IV	Average	
days	*gms.*											
1	5	1255	982	832	631	925	641	626	505	359	533	631
3	8	1457	1367	1206	913	1236	767	928	867	571	783	896
6	11	1374	1451	1549	1221	1399	1047	967	1053	800	967	1075
9	10	1451	1734	1994	2013	1798	914	1308	1459	1428	1277	1407
12	13	1553	1812	1910	2157	1858	818	1210	1602	1499	1282	1426
15	13	1598	1618	1902	2128	1812	815	1178	1595	1559	1287	1418
20	29	1627	1764	1972	2189	1888	894	1215	1606	1960	1419	1536
Av. 11	14	1510	1624	1756	1770	1665	876	1134	1364	1303	1169	1293
25	36	1540	1655	1909	1995	1775	834	1243	1539	1702	1330	1441
50	59	1497	1611	1821	1924	1713	805	1204	1580	1906	1374	1459
100	112	1353	1550	1744	2018	1666	837	1306	1510	1737	1348	1428
150	183	1362	1497	1683	1917	1615	832	1150	1803	1917	1426	1473
257	137	1345	1524	1738	1976	1646	873	1230	1555	1927	1396	1459
366	181	1290	1561	1817	2297	1741	893	1239	1651	1844	1407	1491
546	255	1266	1486	1772	2257	1695	831	1336	1650	1839	1414	1484
Av. 213	138	1379	1555	1783	2055	1693	844	1244	1613	1839	1385	1462
Ratios 1– 12 days						1 : 2.0					1 : 2.4	1 : 2.3
1– 20 "						: 2.0					: 2.7	: 2.4
1–546 "						: 1.8					: 2.7	: 2.4
20–546 "						: 0.9					: 1.0	: 0.9
1– 11 "						: 1.8					: 2.2	: 2.0
11–213 "						: 1.0					: 1.2	: 1.1

At first we shall consider the weighted volume for the cell bodies of the inner and outer hair cells combined (chart 33). As table 67 shows, the volume increases continuously to the full size at twenty days. From one to twelve days the increase is rapid, and after that the volumes are about the same, though somewhat fluctuating. The ratios show this relation clearly.

Condensing all age groups into three (averages in table 67), then the relation changes somewhat. From one to eleven days the volume increases more than 100 per cent, while from eleven to 213 days it increases only 13 per cent.

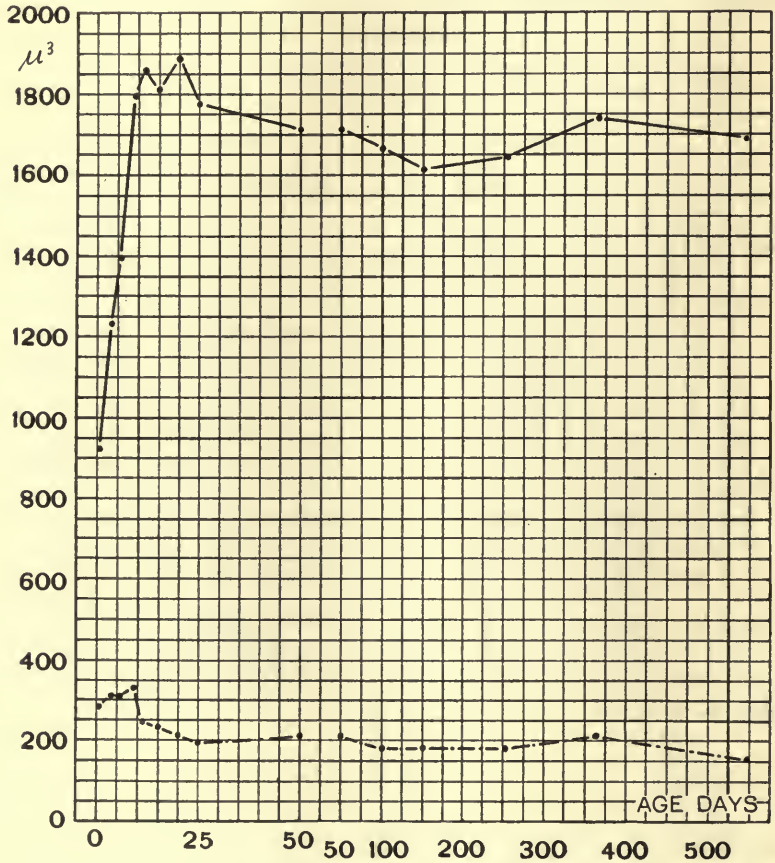

Chart 34 The volume of inner hair cells and of their nuclei, tables 67 and 69.
———— Volume of inner hair cells.
-·-·-·-·-· Volume of nuclei of inner hair cells.

The data for the growth of the nuclei of the inner and outer hair cells are presented in tables 68 and 69. The weighted values for the diameters of the nuclei (table 68) are large at the earlier stages, but from twelve days decrease gradually till

old age. In the three condensed age groups (averages) we see the decrease of the values from birth till old age. In table 69 are given the values for the volumes of the nuclei, calculated as spheres (chart 33).

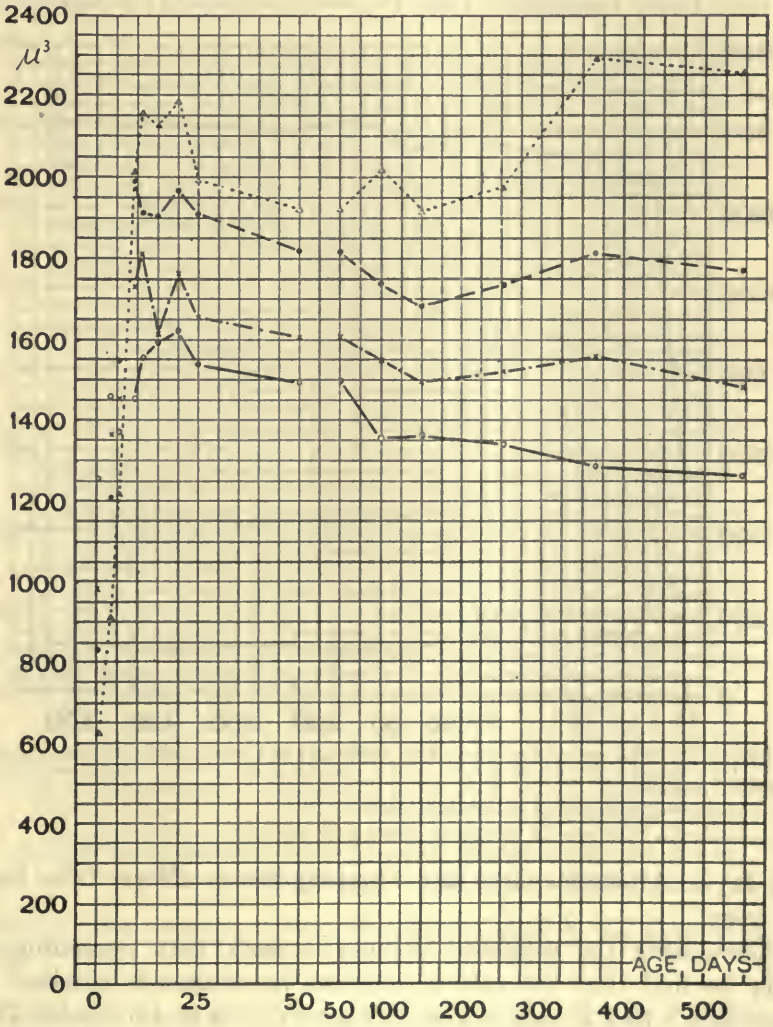

Chart 35 The volume of inner hair cells, according to the turns of the cochlea, table 67.

The weighted values for the volumes of the inner and outer hair cells in each turn are given in μ^3 table 70. At the bottom of each column is given the ratio from 1 to 12, 1 to 20, 1 to 546, and 20 to 546 days of age. While the volume at birth is largest in turn I and smallest in turn IV, that in turn III is largest at

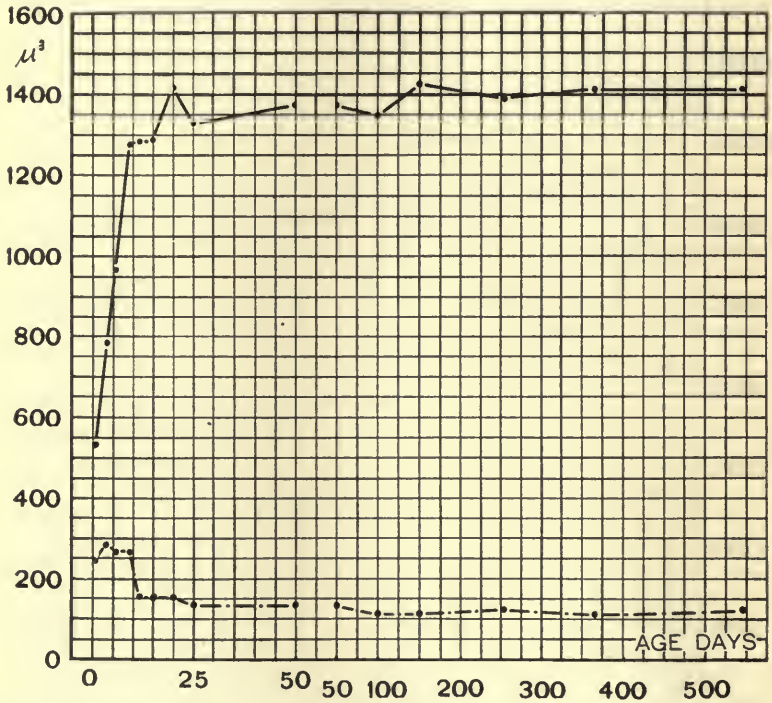

Chart 36 The volume of outer hair cells and of their nuclei, in cubic micra, tables 67 and 69.

———— Volume of outer hair cells.

–·–·–·–·– Volume of nuclei of outer hair cells.

six days. After nine days the volume increases always from base to apex.

Comparing the weighted volume in each turn according to age, we find that the rate of increase in volume is smallest in turn I (1.3 to 1.2) and largest in turn IV (3.9 to 4.6) (table 70).

In table 72 are given the weighted values for the diameters of the nuclei of the inner and outer hair cells in each turn. They

increase and then decrease during the first twelve days. The rate of decrease is largest in turn I, and smallest in turn IV, as the ratios at the bottom of each column show. That the diameters at

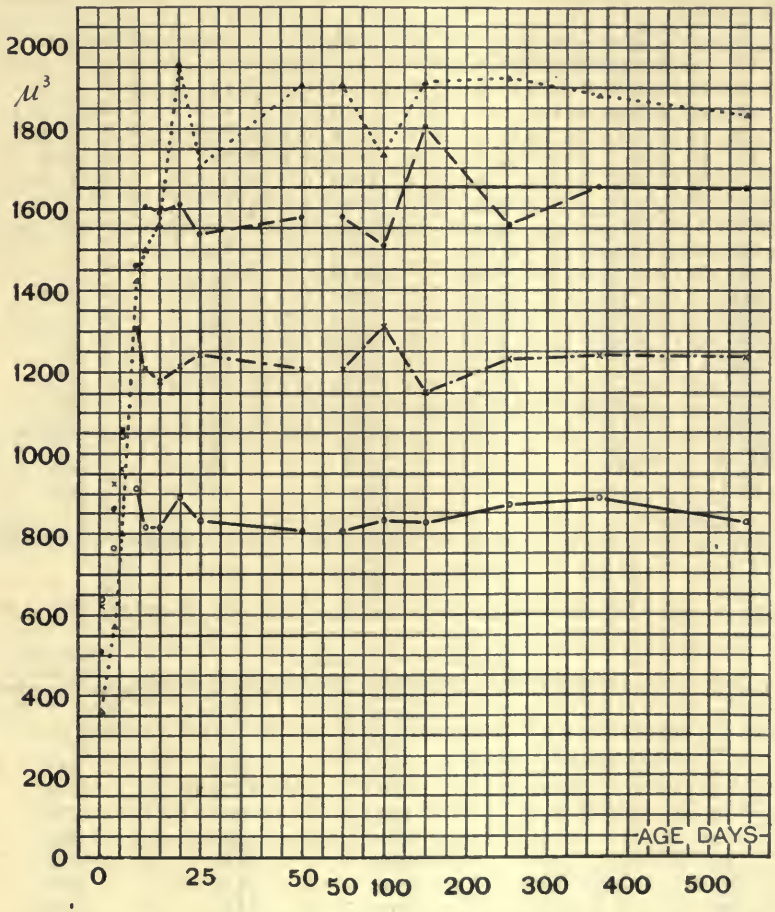

Chart 37 The volume of outer hair cells, according to the turns of the cochlea, table 67.

the later ages have about the same value in each turn, or are a little larger in the upper than in the lower turn, is to be seen in table 73.

TABLE 68

Mean diameters of the nuclei of the inner and outer hair cells—in μ

AGE	BODY wght	DIAMETERS—NUCLEI OF THE INNER HAIR CELLS — Turns of the cochlea— μ					DIAMETERS—NUCLEI OF THE OUTER HAIR CELLS — Turns of the cochlea— μ					WEIGHTED AVERAGE
		I	II	III	IV	Average	I	II	III	IV	Average	
days	*gms.*											
1	5	8.6	8.3	7.8	7.8	8.1	7.7	8.1	7.4	7.6	7.7	7.8
3	8	8.6	8.5	8.2	7.8	8.3	8.3	8.4	8.1	7.5	8.1	8.2
6	11	8.5	8.6	8.3	8.0	8.3	8.0	8.0	8.1	7.9	8.0	8.1
9	10	8.7	8.5	8.2	8.7	8.5	7.6	7.9	8.4	8.2	8.0	8.1
12	13	7.6	7.7	7.5	7.9	7.7	5.8	6.5	6.8	7.4	6.6	6.9
15	13	7.5	7.5	7.7	7.9	7.6	6 1	6.6	6.8	7.0	6.6	6.9
20	29	7.0	7.3	7.6	7.8	7.4	6.0	6.4	6.9	7.3	6.6	6.8
Av. 11	14	8.0	8.0	7.9	8.0	8.0	7.0	7.3	7.5	7.6	7.3	7.5
25	36	7.3	7 2	7.2	7.1	7.2	6.0	6.3	6.3	6.5	6.3	6.5
50	59	7.0	7.5	7.3	7.3	7.3	6.0	6.2	6.3	6.7	6.3	6.6
100	112	6.7	7.0	7.1	7 1	7.0	5.8	6.0	6.0	6.0	5.9	6.2
150	183	6.6	6.8	7.0	7.3	6.9	6.0	6.0	6.2	6.1	6.0	6.2
257	137	6.6	6.9	7.0	7.7	7.0	5.9	6.0	6.2	6.4	6.1	6.3
366	181	7.6	7.4	7.3	7.2	7.4	5.9	6.0	6.1	6.0	6.0	6.4
546	255	6.5	6.5	6.5	7.1	6.6	5.8	6.0	6.1	6.4	6.1	6 2
Av. 213	138	6.9	7.0	7.1	7.3	7.1	5.9	6.1	6.2	6.3	6.1	6.3
Ratios 1– 12 days						1 : 1.0					1 : 0.9	1 : 0.9
1– 20 "						: 0.9					: 0.9	: 0.9
1–546 "						: 0.8					: 0.8	0.8
20–546 "						: 0.9					: 0.9	: 0.9

TABLE 69

Average volumes of the nuclei of the inner and outer hair cells (charts 33, 34 and 36)

AGE	BODY WEIGHT	VOLUME OF NUCLEUS—HAIR CELLS — Inner	Outer	WEIGHTED VOLUMES—INNER AND OUTER HAIR CELLS
days	*gms.*	μ^3	μ^3	μ^3
1	5	278	239	248
3	8	299	278	289
6	11	299	268	278
9	10	322	268	278
12	13	239	151	172
15	13	230	151	172
20	29	212	151	165
25	36	195	131	144
50	59	204	131	151
100	112	180	108	125
150	183	172	113	125
257	137	180	119	131
366	181	212	113	137
546	255	151	119	125
Ratios 1– 12 days		1 : 0.9	1 : 0.6	1 : 0.7
1– 20 "		: 0.8	: 0.6	: 0.7
1–546 "		: 0.5	: 0.5	: 0.5
20–546 "		: 0.7	: 0.8	: 0.8

The growth of the inner hair cell. The volume of the inner hair cell table 67 (chart 34) increases with age up to twenty

TABLE 70

Weighted volumes of the inner and outer hair cells according to the turns of the cochlea

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ^3			
		I	II	III	IV
days	*gms.*				
1	5	795	715	587	427
3	8	940	1038	952	657
6	11	1129	1088	1177	905
9	10	1048	1415	1593	1574
12	13	1002	1361	1679	1664
15	13	1011	1288	1672	1701
20	29	1052	1352	1698	2017
25	36	1011	1346	1632	1775
50	59	978	1306	1640	1911
100	112	966	1367	1569	1807
150	183	965	1237	1773	1917
257	137	991	1304	1601	1939
366	181	992	1320	1693	1957
546	255	940	1374	1681	1944
Ratios 1– 12 days		1 : 1.3	1 : 1.9	1 : 2.9	1 : 3.9
1– 20 "		: 1.3	: 1.9	: 2.9	: 4.7
1–546 "		: 1.2	: 1.9	: 2.9	: 4.6
20–546 "		: 0.9	: 1.0	: 1.0	: 1.0

TABLE 71—*Condensed*

Ratios of the weighted volumes of the inner and outer hair cells according to the turns of the cochlea

AGE	BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*gms.*			
1	5	1 : 0.9	1 : 0.7	1 : 0.5
8	11	: 1.2	: 1.3	: 1.2
18	21	: 1.3	: 1.6	: 1.8
213	138	: 1.4	: 1.7	: 1.9

days; to nine days rapidly, then slowly. After twenty days it decreases slowly, as do the weighted volumes of the inner and outer hair cells, and with fluctuations, is nearly the same after

100 days. The three condensed age groups show that from 1 to 11 days it has increased 80 per cent, while from 11 to 213 days it has gained less than 2 per cent.

TABLE 72

Weighted diameters of the nuclei of the inner and outer hair cells according to the turns of the cochlea

AGE	BODY WEIGHT	TURNS OF THE COCHLEA— μ			
		I	II	III	IV
days	*gms.*				
1	5	7.9	8.2	7.5	7.7
3	8	8.4	8.4	8.1	7.6
6	11	8.1	8.2	8.2	7.9
9	10	7.9	8.1	8.4	8.3
12	13	6.3	6.8	7.0	7.5
15	13	6.5	6.8	7.0	7.2
20	29	6.3	6.6	7.1	7.4
25	36	6.3	6.5	6.5	6.7
50	59	6.3	6.5	6.6	6.9
100	112	6.0	6.3	6.3	6.3
150	183	6.2	6.2	6.4	6.4
257	137	6.1	6.2	6.4	6.7
366	181	6.3	6.4	6.4	6.3
546	255	6.0	6.1	6.2	6.6
Ratios 1– 12 days		1 : 0.8	1 : 0.8	1 : 0.9	1 : 1.0
1– 20 "		: 0.8	: 0.8	: 0.9	: 1.0
1–546 "		: 0.8	: 0.7	: 0.8	: 0.9
20–546 "		: 1.0	: 0.9	: 0.9	: 0.9

TABLE 73.—*Condensed*

Ratios of the weighted diameters of the nuclei of the inner and outer hair cells— according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*gms.*			
1	5	1 : 1.0	1 : 0.9	1 : 1.0
8	11	: 1.0	: 1.0	: 1.0
18	21	: 1.0	: 1.1	: 1.1
213	138	: 1.0	: 1.0	: 1.1

From nine days on the volume of the inner hair cell increases in passing from the base to the apex. During the earlier stages

there are some fluctuations (table 67, chart 35). In the condensed table 74 the general relations are shown. The growth of the nuclei of the inner hair cells in diameter is given in table 68.

As we see, the diameters increase from birth to nine days, then decrease slowly but steadily. In the three average age groups, however, the values decrease continuously with age. In table 69 are given the values for the volumes of the nuclei of the inner hair cell (chart 34).

TABLE 74—*Condensed*

Ratios of the volume of the inner hair cells according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 0.8	1 : 0.7	1 : 0.5
11	14	: 1.1	: 1.2	: 1.2
213	138	: 1.1	: 1.3	: 1.5

TABLE 75—*Condensed*

Ratios of the diameters of the nuclei of the inner hair cells according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 0.9	1 : 0.9
11	14	: 1.0	: 1.0	: 1.0
213	138	: 1.0	: 1.0	: 1.1

The ratios of the diameters of the nuclei of the inner hair cells decrease at the earlier ages in each turn from the base to the apex. After nine days they are nearly the same in all the turns (tables 68 and 75), though their absolute values decrease in all the turns after nine days.

The growth of the outer hair cells. In general, the changes in the volume of the outer hair cells are like those in the inner hair cells. Therefore, the volume increases strikingly up to nine days of age, then gradually to twenty days. The main dif-

ference is that the volume in the outer hair cells does not diminish so much after twenty-five days, but holds nearly the same value (table 67, chart 36). In condensed age groups, therefore, we see a large increase in the size of the cells with age.

To determine the growth of the outer hair cells in each turn of the cochlea, table 67 is used (chart 37). From twenty days on the values increase from the basal to the apical turn. Before twenty days the relations are irregular or reversed. In table 76 this relation is clearly brought out.

Comparing the changes of the volume of the outer hair cells in three age groups (table 67), we find that the average volume increases throughout each turn with age, except in turn I, where

TABLE 76—*Condensed*

Ratios of the volumes of the outer hair cells according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 0.8	1 : 0.6
11	14	: 1.3	: 1.6	: 1.5
213	138	: 1.5	: 1.9	: 2.2

that at eleven days is largest. In the inner hair cells, however, values at eleven days are largest in both turn I and II.

For the nuclei of the outer hair cells, the diameters are given in table 68). Here the diameters tend to increase from one to nine days. At twelve days they decrease strikingly, and after that very slowly. In table 69 are given the values for the volumes of the nuclei of the outer hair cells.

In table 68 are given also the measurements for the nuclei of the outer hair cells according to the turn of the cochlea. At nine days and after, the diameters become larger in passing from base to apex, while in the earlier stages this relation is irregular or reversed. The decrease of the measurements in, each turn with age is clearly shown in the three age groups.

In table 77 are given the average ratios of turn I to the three other turns.

The comparison of the growth of the inner and outer hair cells. As already stated, the growth of the inner and outer hair cells in volume proceeds in about the same way till they reach their full size at twenty days. After that we note a difference between them. While the outer hair cells maintain a nearly constant volume, the volume of the inner hair cells diminishes

TABLE 77—*Condensed*

Ratios of the diameters of the nuclei of the outer hair cells according to the turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.1	1 : 1.0	1 : 1.0
11	14	: 1.0	: 1.1	: 1.1
213	138	: 1.0	: 1.1	: 1.1

TABLE 78—*Condensed*

Comparison of the volumes of the inner and the outer hair cells

AVERAGE AGE	AVERAGE BODY WEIGHT	AVERAGE VOLUMES—HAIR CELLS		RATIOS OF INNER TO OUTER
		Inner	Outer	
days	*grams*	μ^3	μ^3	
1	5	925	533	1 : 0.6
11	14	1665	1169	: 0.7
213	138	1693	1385	: 0.8

somewhat with age. When we consider the volume according to the three age groups, it increases in both groups throughout life (table 78). There are, however, large differences in the rate of increase. The inner hair cell increases its volume at 11 days by 80 per cent and between 11 and 213 days by less than 2 per cent. For the outer hair cells the increase by 11 days is 120 per cent and from 11 to 213 days, 19 per cent. At the same time the inner are always larger than the outer hair cells, as the ratios in table 78 show.

The diameters of the nuclei in both the inner and outer hair cells diminish in value after nine days of age. This decrease is larger in the outer than in the inner cells. In table 79 are given the values for the diameters of the nuclei in both inner and outer hair cells. In the last column are the ratios between them.

Thus, while the volumes of the outer hair cells, as compared with the inner hair cells, become relatively larger with age (table 78), the diameters of their nuclei become relatively smaller (table 79).

TABLE 79—*Condensed*

Comparison of the diameters of the nuclei of the inner and outer hair cells

AVERAGE AGE	AVERAGE BODY WEIGHT	AVERAGE DIAMETERS OF THE NUCLEI OF THE HAIR CELLS		RATIOS OF THE AVERAGE DIAMETERS OF THE NUCLEI OF THE INNER AND OUTER HAIR CELLS
		Inner	Outer	
days	*grams*	*μ*	*μ*	
1	5	8.1	7.7	1 : 1.0
11	14	8.0	7.3	: 0.9
213	138	7.1	6.1	: 0.9

Comparison of the growth of the inner and outer hair cells according to sex. A careful and elaborate comparison has been made to determine whether there are differences in the growth of the hair cells according to sex.

In table 80 are given the average values for the volumes of the cell bodies and their respective nuclei. No significant differences according to sex were found.

Comparison of the growth of the inner and outer hair cells according to side. The same treatment of the data was followed as in the determination for the influence of sex. In table 81 are given the average values for the volumes of the inner and outer hair cells and their respective nuclei. Again no significant differences according to side were found.

On the nucleus-plasma ratios of the inner and outer hair cells. For the inner and outer hair cells here measured the weighted volumes of the cell bodies and of their nuclei are entered in the condensed table 82, and the ratios of the volume of the nucleus

to that of the cytoplasm (=cell volume less nucleus volume) are given in the last column. This ratio increases with age, as table 82 shows. While the ratio is 1.5 in the youngest and smallest group, it is 9.9 in the largest. This means that as a group these cells are continually growing in volume. This result may be analysed for the two groups of cells involved.

TABLE 80

Average volumes of inner and outer hair cells and of their respective nuclei—in μ^3 according to sex

AGE	BODY	NO. OF RATS	SEX	INNER HAIR CELLS		OUTER HAIR CELLS		WEIGHTED AVERAGE VOLUME	
				Average volume		Average volume			
				Cell	Nucleus	Cell	Nucleus	CELLS	NUCLEI
days	*grams*								
3	7	1	♂	1213	310	815	268	915	278
	8	1	♀	1319	310	888	322	996	319
6	11	2	♂	1426	289	955	278	1073	281
	10	2	♀	1372	310	979	268	1077	278
9	10	2	♂	1701	310	1351	258	1439	271
	9	2	♀	1895	345	1203	278	1376	295
12	14	2	♂	1830	258	1344	157	1466	182
	12	2	♀	1886	221	1221	151	1387	168
100	146	1	♂	1687	180	1342	113	1428	129
	103	1	♀	1779	212	1319	108	1434	184
150	189	1	♂	1679	165	1382	119	1456	131
	154	1	♀	1639	212	1611	119	1618	142
365	205	1	♂	1739	258	1389	119	1477	154
	170	1	♀	1659	221	1486	113	1529	140
Volume greater in male				3	2	3	4	5	3
Volume greater in female				4	4	4	2	2	4
Equal				0	1	0	1	0	0

The nucleus-plasma ratio of the inner and outer hair cells considered separately. This is shown for the inner hair cells in table 83. The ratios are also progressive, but somewhat larger for the earlier age groups and smaller for the oldest, than in the previous instance.

The ratios for the outer hair cells are also progressive, and the range is greater than for the inner hair cells as table 84 shows. Here the ratio is 1.2 for the youngest group and 10.6 for the

oldest. This indicates that at one day and eleven days the relative volume is less in the outer than in the inner hair cells, but at the later age the outer hairs cells grow more.

TABLE 81

Volumes of the inner and outer hair cells and of their respective nuclei according to side in μ^3

AGE	BODY WEIGHT	NO. OF RATS	SIDE	INNER HAIR CELLS Average volume		OUTER HAIR CELLS Average volume		WEIGHTED AVERAGE VOLUME	
				Cell	Nucleus	Cell	Nucleus	CELLS	NUCLEI
1	5	2	R.	895	299	555	248	640	261
			L.	955	268	511	230	622	239
3	7	1	R.	1213	310	815	268	915	278
			L.	1395	299	920	299	1039	299
6	11	2	R.	1381	322	1010	278	1103	289
			L.	1416	289	923	258	1046	268
9	9	2	R.	1782	310	1177	268	1328	278
			L.	1815	333	1378	268	1487	284
12	12	1	R.	1887	212	1310	151	1454	166
			L.	1885	221	1132	151	1320	168
15	13	1	R.	1895	230	1522	144	1615	165
			L.	1848	239	1419	151	1526	172
20	29	2	R.	1914	212	1365	144	1502	161
			L.	1862	221	1472	165	1570	179
25	36	2	R.	1758	204	1307	131	1420	149
			L.	1792	195	1351	131	1461	147
50	59	2	R.	1741	204	1443	125	1518	145
			L.	1687	204	1305	137	1401	154
100	102	2	R.	1675	187	1355	113	1440	131
	123	2	L.	1658	172	1339	113	1419	128
150	189	1	R.	1565	172	1420	113	1456	128
			L.	1679	165	1382	119	1456	131
257	137	2	R.	1685	187	1377	125	1454	140
			L.	1607	180	1416	119	1464	134
367	175	2	R.	1634	195	1436	113	1486	134
365	188	2	L.	1848	230	1374	113	1493	142
546	255	2	R.	1831	157	1474	119	1563	128
			L.	1559	151	1353	119	1405	127
Volume greater on right side				7	8	9	3	7	6
Volume greater on left side				7	5	5	5	6	8
Equal				0	1	0	6	1	0

This seems to be important and to illustrate the fact that in the papilla spiralis the growth of the elements lying nearer the axis occurs earlier than that of the elements nearer the periphery.

TABLE 82—*Condensed*

Nucleus-plasma ratios of the inner and outer hair cells—μ^3

AVERAGE AGE	AVERAGE BODY WEIGHT	AVERAGE VOLUME OF INNER AND OUTER HAIR CELLS		VOLUME OF CYTOPLASM	NUCLEUS-PLASMA RATIOS
		Cell	Nucleus		
days	*grams*				
1	5	631	248	383	1 : 1.5
11	14	1293	226	1067	: 4.7
213	138	1462	134	1328	: 9.9

TABLE 83—*Condensed*

Nucleus-plasma ratios of the inner hair cells—μ^3

AVERAGE AOE	AVERAOE BODY WEIGHT	AVERAGE VOLUME OF INNER HAIR CELLS		VOLUME OF CYTOPLASM	NUCLEUS-PLASMA RATIOS
		Cell	Nucleus		
days	*gms.*				
1	5	925	278	647	1 : 2.3
11	14	1665	268	1397	: 5.2
213	138	1693	187	1506	: 8.1

TABLE 84—*Condensed*

Nucleus-plasma ratios of the outer hair cells

AVERAGE AGE	AVERAOE BODY WEIGHT	AVERAGE VOLUME OF OUTER HAIR CELLS		VOLUME OF CYTOPLASM	NUCLEUS-PLASMA RATIOS
		Cell	Nucleus		
days	*grams*				
1	5	533	239	294	1 : 1.2
11	14	1169	204	965	: 4.7
213	138	1385	119	1266	: 10.6

17. Deiters' cells. The Deiters' cells are most delicate elements. In the literature, so far as I know, there are no exact observations touching the growth of these cells in the papilla spiralis, except a few data for their length. They have an

irregular form and consist of three parts, the phalangeal process, cell body, and foot. The phalangeal process is thin, somewhat crooked in the adult though it runs straight at an earlier stage. As the boundary between this process and the cell body, we take a line running through the supporting cup ('Stutzkelch' of Held) parallel to the plane of the basilar membrane (fig. 10). The cell body in its upper part is wide, including here a round nucleus. It then becomes thin and passes over to the foot. Thus it is almost impossible to get the true volume of the cells. Therefore, we have determined the volume of the cell body only, excluding that of the phalangeal process.

We think of the cell body as a cylinder having an average diameter, which is calculated from four diameters measured at four levels. The first level is just below the upper boundary of the cell body, the second in the widest part, the third below at about the middle of the cell body, and the last is at the narrowest part near the foot.

The height of the cylinder is the length of the cell body within the limits just noted. Thus the volume obtained approximates the value for the natural size of the cell body without the process.

In table 85 (chart 38) are given the values for the volumes of the Deiters' cells thus computed and the diameters and volumes of the nuclei according to age. As there are in the radial section three rows of cells, the values given are, of course, the average of these. At the bottom of the last column appear the ratios at 1 to 12, 1 to 20, 1 to 546, and 12 to 546 days. As we see, the volume of the cell body increases throughout life, slowly during the first nine days, but from twelve to twenty days very rapidly, and then less rapidly to old age.

While the ratio from one to twelve days is 1:5.4, that from 1 to 546 days is 1:29.1, or more than five times as large.

When we consider the volumes of the cells in each turn of the cochlea, we see that it is smallest in turn I and largest in turn IV, though there are some exceptions before nine days of age. Table 86 shows these relations.

The diameters of the nuclei of the cells grow, after some fluctuations in the values at earlier stages, very slowly to old

age, as indicated in table 85 and chart 38. The ratios at the bottom of the corresponding column show these relations. The values for the volumes of the nuclei of the cells are given in the last column. Here, also, the diameters in the upper turns tend to be larger than in the basal turn. In table 87 are given the ratios of the diameters of turn I to the three other turns. We see in all the turns about the same ratios, 1:1.0.

In the literature we find but two observations on the diameters of the nuclei of the Dieters' cells. Kolmer ('07) reports in the pig 5 μ, and von Ebner ('02) gives in man 7 μ for the diameter of the round nucleus of the cells.

In the rat, therefore, the diameter is larger than in these two forms, but no significance can be attached to this difference until correction has been made for the several techniques employed. This I am unable at present to do.

On the nucleus-plasma ratio in Deiters' cells. In the condensed table 88 are given the volumes of the cell bodies and of their nuclei together with the respective nucleus-plasma ratios. This shows that the ratio is progressive with age. While the ratio is at birth only 0.05, that in the oldest group is 28.3. The absolute increase is not great at earlier stages, but by eighteen days it is marked

The rapid change in the ratio is very interesting. Before eight days of age the cells are still immature. Some time after eight days they develop rapidly, seeming to play some important part in the special functions of the cochlea.

On the length of Deiters' cells. To measure the length of Deiters' cells we divide them into two parts, the upper and the lower, by the boundary line between the cell body and the phalangeal process. The sum of these two lengths makes the total length of the cells.

In table 89 are given the values for the total length and for each part separately (chart 39). As in the volume of the cells, we see an astonishing change in the development of the length. The length of the cells increases through life, at earlier stages a little, but at twelve days it becomes nearly twice as long as at nine days. The ratios at the bottom of the last column show the course of growth.

TABLE 85

The volume of Deiters' cells and the mean diameters and volumes of their respective nuclei (chart 38)

AGE	BODY WEIGHT	VOLUME OF THE DEITERS' CELLS μ^3					NUCLEI Diameters					VOLUMES
		I	II	III	IV	Average volume	I	II	III	IV	Average diameters μ	Average volumes μ^3
days	*grams*											
1	5	278	232	237	256	251	7.6	7.5	7.5	8.1	7.7	239
3	8	290	309	349	352	325	7.0	7.0	6.9	7.0	7.0	180
6	11	425	395	495	364	420	7.0	6.5	6.7	6.6	6.7	165
9	10	635	461	554	423	518	6.9	7.0	7.1	7.1	7.0	180
12	13	1122	1369	1395	1569	1364	6.5	7.0	6.9	7.1	6.9	180
15	13	1466	2187	2659	3127	2359	7.0	7.2	7.2	7.3	7.2	195
20	29	3576	4271	5740	6171	4939	7.6	7.8	7.9	7.9	7.8	248
25	36	4088	4467	5470	5757	4695	7.3	7.2	7.3	7.4	7.3	212
50	59	4839	5970	6258	6816	5971	7.3	7.5	7.5	7.4	7.4	212
100	112	5011	6083	7137	6607	6210	6.9	7.6	7.5	7.4	7.3	212
150	183	5755	6291	7657	6750	6613	7.5	7.6	7.5	7.1	7.4	212
257	137	5776	6540	8841	8544	7425	7.4	7.8	7.9	8.0	7.8	248
366	181	6163	6908	7701	7895	7167	7.4	7.7	7.9	7.9	7.7	248
546	255	6092	6919	8028	8152	7298	7.4	7.9	8.0	7.7	7.7	248
Ratios	1— 12 days					1 : 5.4					1 : 0.9	
	1— 20 "					: 19.7					: 1.0	
	1—546 "					: 29.1					: 1.0	
	12—546 "					: 5.4					: 1.1	

TABLE 86—*Condensed*

Ratios of volumes of the Deiter's cells according to turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 0.8	1 : 0.9	1 : 0.9
8	11	: 1.0	: 1.1	: 1.1
18	21	: 1.3	: 1.7	: 1.8
213	138	: 1.1	: 1.4	: 1.3

TABLE 87—*Condensed*

Ratios of the diameters of the nuclei of Deiters' cells according to turns of the cochlea

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS		
		I–II	I–III	I–IV
days	*grams*			
1	5	1 : 1.0	1 : 1.0	1 : 1.1
8	11	: 1.0	: 1.0	: 1.0
18	21	: 1.0	: 1.0	: 1.0
213	138	: 1.0	: 1.1	: 1.0

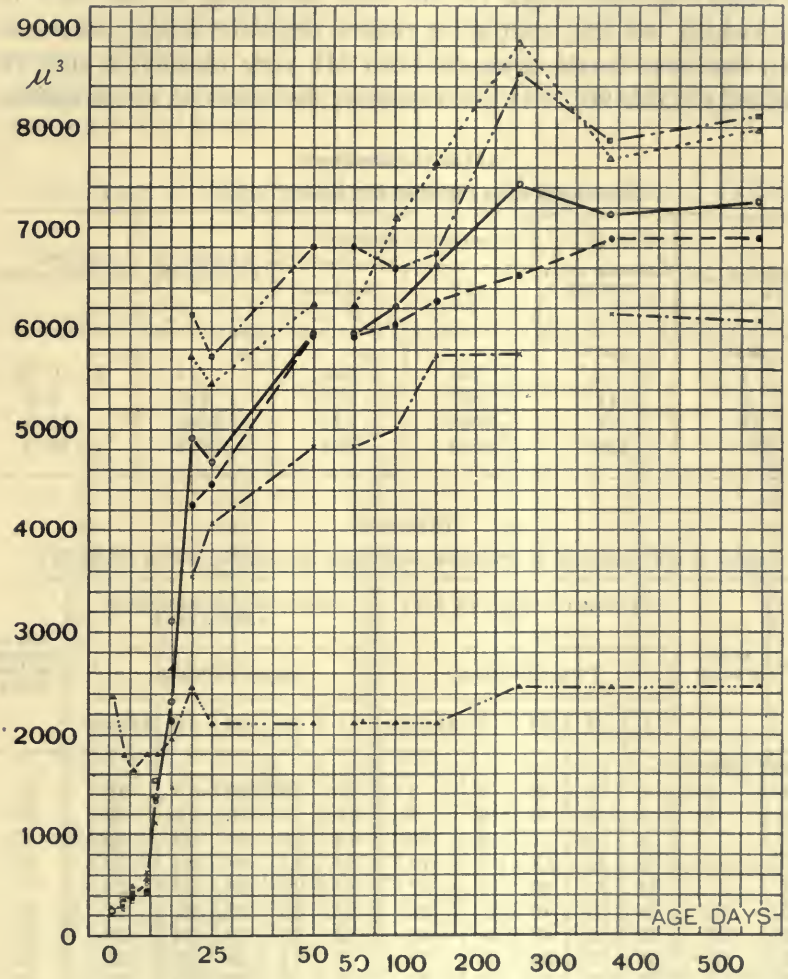

Chart 38 Showing the volume of Deiters' cells and their nuclei, on the average and according to the turns of the cochlea, table 85.

———— Average volume of Deiters' cells.
-.-.-.-.-. Volume of the cells in about the middle of the basal turn.
---------- Volume of the cells in about the beginning of the middle turn.
. . . . . Volume of the cells in about the middle of the middle turn.
-.-.-.-.- Volume of the cells in about the beginning of the apical turn.
-.-.-.-.-. Average volume of nuclei of Deiters' cells, × 10.

Comparing the length of the cells according to the turn of the cochlea, we find that after twelve days the length increases from the base to the apex, in turn III very rapidly, in turn IV gradually (table 90). At earlier stages the relations are irregular.

TABLE 88—*Condensed*

Nucleus-plasma ratios of the Deiters' cells

AVERAGE AGE	AVERAGE BODY WEIGHT	AVERAGE VOLUMES		VOLUME OF CYTOPLASM μ^3	NUCLEUS-PLASMA RATIOS
		Cell μ^3	Nucleus μ^3		
days	*grams*				
1	5	251	239	12	1 : 0.05
8	11	657	172	485	: 2.8
18	21	3649	221	3428	: 15.5
213	138	6483	221	6262	: 28.3

TABLE 89

Length of cell body and of processus phalangeus of Deiters' cells μ (chart 39)

AGE	BODY WEIGHT	LENGTH OF THE CELL BODY					LENGTH OF THE PROCESSUS PHALANGEUS					TOTAL LENGTH OF THE CELLS
		Turns of cochlea					Turns of cochlea					
		I	II	III	IV	Average	I	II	III	IV	Average	
days	*gms*											
1	5	8	8	8	9	8	20	19	20	15	19	27
3	8	8	9	9	10	9	16	17	18	18	17	26
6	11	9	9	11	10	10	19	22	23	22	22	32
9	10	18	12	13	11	14	18	21	26	24	22	36
12	13	31	35	40	43	37	18	22	29	25	24	61
15	13	34	37	40	43	39	21	25	32	31	27	66
20	29	39	41	49	49	45	19	23	30	34	27	72
25	36	42	43	51	51	47	17	21	30	32	25	72
50	59	41	45	53	53	48	16	22	30	34	26	74
100	112	43	45	54	53	49	17	25	29	31	26	75
150	183	45	46	53	52	49	17	22	32	34	26	75
257	137	43	46	56	58	51	18	24	28	31	25	76
366	181	43	48	55	55	50	17	23	29	32	25	75
546	255	46	49	56	56	52	16	23	30	33	26	78
Ratios	1— 12 days					1 : 4.6					1 : 1.3	1 : 2.3
	1— 20 "					: 5.6					: 1.4	: 2.7
	1—546 "					: 6.5					: 1.4	: 2.9
	12—546 "					: 1.4					: 1.1	: 1.3

When we consider the length of the cell body, it is remarkable that the increase takes place so rapidly. While at 1 day it measures only 8 μ and at nine days only 14 μ, it increases very suddenly at twelve days of age, and after that slowly but continuously (table 89).

TABLE 90

Total length of Deiters' cells according to turns of the cochlea—μ (chart 39)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA			
		I	II	III	IV
days	*grams*				
1	5	28	27	28	24
3	8	24	26	27	28
6	11	28	31	34	32
9	10	36	33	39	35
12	13	49	57	69	68
15	13	55	62	72	74
20	29	58	64	79	83
25	36	59	64	81	83
50	59	57	67	83	87
100	112	60	70	83	84
150	183	62	68	85	86
257	137	61	70	84	89
366	181	60	71	84	87
546	255	62	72	86	89

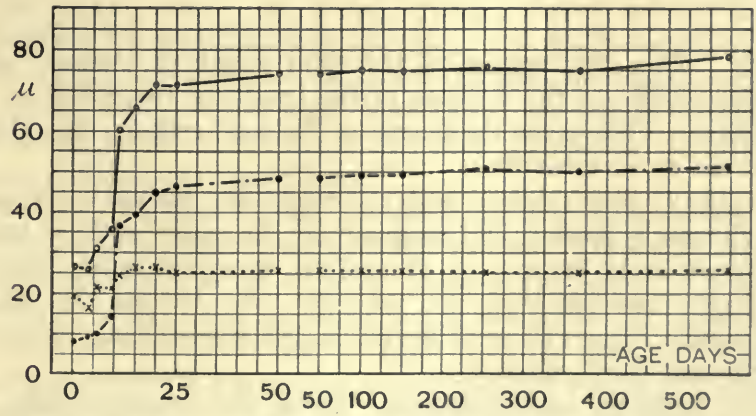

Chart 39 The length of Deiters' cells, tables 89 and 90.

———— Total length of the cells.

-·-·-·-·-·- Length of the cell bodies.

..... Length of processus phalangeus.

In the ratios at the bottom of table 89 this is shown very evidently and in each turn this relation is to be seen.

For the length of the phalangeal process the story is quite different. It increases from birth to twelve days a little; at fifteen days it reaches full size, and then holds its value (table 89). After three days the length is smallest in turn I and largest in turn IV. This relation lasts to old age.

Comparing the growth of the length of the cell body and phalangeal process, there is a large difference between them. While the length in the phalangeal process is at birth over twice that of the cell body, at 546 days it is only half that of the cell

TABLE 91

Total length of Deiters' cells—in μ (Retzius)

AGE	RABBIT				CAT			
	Basal turn	Middle	Apical	Average	Basal	Middle	Apical	Average
days								
New-born	48	70	60	59	45	65	48	53
2	45	66	54	55	—	—	—	—
3	—	—	—	—	45	60	—	—
7	80	90	75	82	49	69	63	60
10	98	100	114	104	—	—	—	—
11	—	—	—	—	75	90	45	70
14	84	105	112	100	—	—	—	—
30	—	—	—	—	54	75	70	66

Thus the increase of the total length of Deiters' cells is due chiefly to the increase in the length of the cell body.

Retzius ('84) gives the length of Deiters' cells in the rabbit and cat as in table 91.

Table 91 shows that in both the rabbit and the cat the length at all ages is greater, and especially at the earlier stage is twice as great, as in the rat. In the rabbit there is a rapid increase in length between seven and ten days. For the cat the values are smaller, nearer those of the rat, and show less change between birth and thirty days.

18. Summary and discussion. Using the foregoing data on the form and measurements of the elements of the cochlear duct, I desire here to summarize the results and to discuss the consequent changes in the form of the organ of Corti (table 92).

We have already noted that at birth the greater epithelial ridge constitutes the main part of the tympanic wall, and the lesser epithelial ridge, from which arises later the most important organ, is represented by a small and undeveloped prominence. With age this greater ridge disappears gradually and is transformed into a furrow lined with low epithelial cells, the sulcus spiralis internus (Waldeyer). These changes appear first at the base and then pass gradually to the upper turns. In the lesser ridge also there are important developmental changes. At first the hair cells and pillar cells grow, and just before the special function appears, striking changes are seen in Deiters' and Hensen's cells. These increase, especially in their length, very rapidly.

Thus the papilla spiralis, which hitherto had its highest point at the summit of the arch of Corti, shows a remarkable change of form, as the outer part of the papilla increases its height, so that finally Hensen's cells mark the highest point in the papilla. The surface then ceases to be parallel to the basilar membrane, and slopes inward, making with the basilar membrane an acute angle opening outward. At the same time the papilla spiralis appears to be shifted inward—i.e., towards the axis.

Kölliker has described how the cells, from which the pillars or rods of Corti arise, at first stand nearly parallel, but later separate at their base. He thought that this "von einem Längenwachstum (?) der Zellen selbst oder ihrer Grundlage, der Membrana basilaris, abhängen kann."

Hensen ('63) first studied this interesting problem in the ox and found it to depend on a peculiar process. He regarded the inward migration as taking place chiefly in the inner pillar cell. The outer pillar cell in the upper turn moves somewhat outward; in the base, however, inward. Moreover, the outer pillar cell increases its length during the development of the papilla much more than the inner does. Thus the summit of the arch of Corti and therefore the papilla spiralis shifts inward on the basilar membrane.

TABLE 92

Summary table giving the fundamental measurements. The values are in micra, usually rounded, except in one instance where they are in degrees

Age in days	1	3	6	9	12	15	20	100	546
Body weight, grams	5	8	11	10	13	13	29	112	255
Body length, mm.	48	56	63	58	70	75	95	159	213
Radial distance between spiral ligaments—μ (table 2) *a* I–II	1410	1560	1650	1635	1640	1655	1645	1663	1680
b III–IV	925	1025	1175	1225	1233	1235	1250	1270	1265
c Average	1168	1293	1413	1430	1437	1445	1448	1467	1473
Radial distance between labium vestibulare and habenula perforata	115	114	115	118	117	122	122	122	119
Breadth of membrana basilaris (table 9) Inner zone	49	63	77	79	88	87	86	92	94
Outer zone	75	91	105	111	100	102	106	106	113
Total	124	154	182	190	188	189	192	198	207
Breadth of membrana tectoria (table 4) Inner zone	37	94	105	123	126	124	129	132	132
Outer zone	140	134	154	158	157	160	162	162	163
Total	177	228	259	281	283	284	291	294	295
Thickness (table 4)	12	32	32	27	25	28	38	36	34
Distance from hab. perf. to foot of inner pillar (table 15)	22	27	0	0	0	0	0	0	0
From hab. perf. to outer corner of inner pillar	30	38	43	42	22	18	15	14	15
Distance between the inner and outer pillars	10	12	18	18	42	48	58	63	63
Distance from hab. perf. to the inner corner of the outer pillar	40	50	61	60	63	67	72	77	78
Basal width of inner pillar (table 19)	—	—	29	31	21	19	15	14	15
Basal width of outer pillar (table 29)	—	—	14	18	21	20	14	15	16
Greatest height of greater epithelial ridge (table 38)	66	53	40	40	45	50	58	55	53
Height from basal plane to surface of pillar cells (table 46)	37	29	30	34	47	51	62	60	59
Length of inner pillar without head (table 61)	29	25	36	39	40	43	52	49	49
Length of outer pillar without head (table 61)	28	23	31	34	51	54	62	59	59
Height of tunnel of Corti (table 49)	—	—	—	—	35	38	47	47	44

Length of inner hair cells	26	24	27	30	33	33	31	28	29
Diameters of nuclei (table 68)	8.1	8.3	8.3	8.5	7.7	7.6	7.4	7.0	6.6
Length of outer hair cells	19	18	22	22	23	26	26	26	26
Diameters of nuclei (table 68)	7.8	8.2	8.1	8.1	6.9	6.9	6.8	6.2	6.2
Height of papilla spiralis at third series of outer hair cells (table 52)	34	24	24	28	50	58	69	67	64
Total length of Deiters' cells (table 89)	27	26	32	36	61	66	72	75	78
Height of Hensen's supporting cells (table 55)	35	21	20	23	51	60	75	83	86
Angle of lam. retic. with membr. basil. in degrees (table 58)	—	—	—	—	10	13	13	15	17
Spiral ganglion (table 95)									
Diameter—cells	10.5	11.5	12.9	13.6	13.8	14.9	18.1	16.9	16.9
Diameter—nuclei	7.9	8.0	8.4	8.5	8.5	8.7	10.2	9.5	9.4
Vestibular ganglion (table 115)									
Diameter—cells	20.3	22.9	23.0	23.9	23.9	23.9	24.1	24.7	25.3
Diameter—nuclei	11.7	12.0	11.9	12.0	12.1	12.0	11.9	12.3	12.2

Böttcher ('69, '72) disagreed with Hensen, though he has confirmed, as did Middendorp ('67), the striking inward spreading of the base of the inner pillar cell.

Gottstein (’72) held that the inner pillar cell does not move inward, but that the increase in the length of the labium tympanicum may explain the peculiar approach of the habenula perforata to the arch of Corti.

Retzius ('84) agreed in general with Hensen's assertion that in the course of development the surface of the sense organ comes to lie under the basal surface of the membrana tectoria. He thought that this change of position is brought about "weniger in dem Verhalten der Pfeilerzellen, sondern vor allem in dem starken Wachstum der Deitersschen Zellen und der von aussen andrückenden Hensenschen Stützzellen,' and that, further, "vielleicht die Membrana tectoria selbst durch eigenes Wachstum und durch Vergrösserung des Limbus mit seinem Vorsprüngen" contributes to this.

Held ('09) agrees with Hensen on the whole.

Prentiss ('13, p. 450) denies the wandering of the spiral organ as follows: "There is no necessity for, and my preparations afford no proof of, an inward shifting of the spiral organ and a consequent displacement of the membrana tectoria."

Hardesty ('15, pp. 60 and 61) discussed the relative position of the spiral organ with reference to the basal surface of the tectorial membrane and says "the developed spiral organ acquires its position well under the basal surface of the tectorial membrane almost entirely by being carried axisward during the completion of the membrane." "In the apical turn, where these changes are greatest, the hair cells of the organ may be carried axisward a distance nearly half the width of the membrane. The upgrowth of the outer supporting cells also forces axisward the apical ends of the elements of the spiral organ and in this way contributes a small part to the shift in the relative position of the hair cells. A slight increase in width of the vestibular lip of the spiral limbus may contribute a still smaller part by extending the membrane outward."

I obtained from the measurements given in the tables the following results concerning the position of the papilla spiralis under the basal surface of the tectorial membrane.

As already stated, since the habenula perforata may be considered after birth as a punctum fixum (Hensen), it is found that the inner pillar cell shifts inward at its inner basal corner during the earlier stage of life. At six days of age it almost always reaches the habenula perforata in the basal turn, though not yet in the apical. At nine days there is no distance between the habenula perforata and the inner corner of the inner pillar cell.

Gottstein's assumption (no measurements) that the labium tympanicum grows outward and approaches to the arch of Corti is not applicable to the rat, as shown by my tables.

The outer pillar cell also moves outward in all the turns through life, but only slightly after nine days. This result does not agree with that of Hensen ('63), who found in the ox the outer pillar cell to move inward a little at the base, not at all in the middle turn and outward at the apex. Böttcher's outward movement of the outer pillar cell at the hamulus in the cat is 90 μ and much larger than in the rat.

Contrary to Hensen, Retzius ('84) also finds in the rabbit an outward movement of the base of the outer pillar cell throughout all the turns. On the other hand, during the earlier stages of development, the top of the arch of Corti moves outward from the labium vestibulare through the outward pressure of the greater epithelial ridge. At this stage the main part of the membrana tectoria does not yet reach to the sense cells, though the part produced from the lesser epithelial ridge spans the spiral organ and connects with the outer part of the papilla.

After nine days of age the condition of the organ is quite different. The most remarkable anatomical changes from the earlier condition are the rapid increase in the length of the outer pillar cells, in the height of the pillar cells above the basilar membrane, in the height of the papilla spiralis at the third series of the outer hair cells, in the height of Deiters' cells, and in the height of Hensen's supporting cells. Also the tunnel of Corti appears.

The greater epithelial ridge has already disappeared in large part and been replaced by a furrow. Pressure displacement of tissue in the direction of the least resistance is common in organogenesis. Thus the inner pillar cell is subject to pressure by the rapid growth of the outward lying and greater part of the papilla spiralis and moves in the direction of the least resistance, therefore inward; the head most and the base not at all. As shown in table 44, the rapid decrease in the radial distance between the labium vestibulare and the head of the inner pillar cell is very evident. The arch of Corti changes its form, now inclining inward, instead of outward as heretofore. The lamina reticularis runs not parallel to the basilar membrane, but ascends outward. The tunnel of Corti also changes more or less its form. Nuel's space now appears possibly as a result of this displacement of the papilla spiralis. Thus we see a change in the position of the sense organ with reference to the membrana tectoria.

With the inward shifting of the papilla, the hair cells come under the basal surface of the membrana tectoria. It is probable that the increase of the relative length of the membrane also takes part in this, since the increase in the breadth of the inner zone of the membrana tectoria from one to twelve days is as 1:3.4 (table 4), while the increase in the breadth of the basilar membrane is as 1:0.5 during the same interval (table 7).

Prentiss' ('13) statement that an inward shifting of the papilla spiralis and a consequent displacement of the membrana tectoria does not take place (in the pig) is not applicable to the rat.

In the rat the labium vestibulare and the inner edge of the head of the inner pillar cell are also two definite points in the same sense, and using them we see an inward shifting of the organ of Corti. I imagine that his observation may have misled him, since the tectorial membrane arises in his preparations from both greater and lesser epithelial ridges, and from the earlier stages covers with its outer part the papilla spiralis. Thus the shifting of the organ inward does not necessitate a change in the position of the papilla with reference to the membrane. In his study of the tectorial membrane in the same animal (pig), Hardesty ('13) describes a large displacement of the papilla spiralis inward.

According to him, the shifting of the organ consists of, 1, the moving axisward of the organ itself, and this constitutes the main shift; 2, the upgrowth of the outer supporting cells, and this contributes a small part to the shift, and, 3, a slight increase of the vestibular lip of the spiral limbus which may contribute a still smaller part. The relation in the rat, however, is different. The moving inward of the papilla itself is not seen in the rat. In the earlier stages the inner basal corner of the inner pillar cell alone shifts inward and reaches the habenula perforata. On the other hand, the outer pillar cell moves outward and the head of the inner pillar cell also, at earlier stages, towards the cells of Hensen. Therefore, during the earlier stages the arch of Corti moves rather outward, owing to the pressure of the growth of the greater epithelial ridge. Since the habenula perforata is to be regarded as a fixed point, the inward displacement of the head of the arch of Corti and of the papilla spiralis is not due to the active shifting inward of the organ itself, as Hardesty ('15) thinks, but to the disappearance of the greater ridge and the passive pressure exerted by the upgrowth of the outer pillar cells and Deiters' and Hensen's cells. The vestibular lip of the spiral lamina and the tectorial membrane itself both increase in their length a little, and these increases play some part in the change of the position of the papilla spiralis with reference to the basal surface of the tectorial membrane.

The membrana basilaris is not concerned with the moving inward of the organ. It increases its length with age in all the turns, but we do not find the change in the position of the feet of the pillar cells on the membrane in such a sense that the feet move inward on it.

Thus the shifting of the papilla spiralis inward in the rat during the development takes place rather in the manner described by Retzius.

Hardesty ('15) states that in the apical turn of the cochlea the organ may be moved axisward a distance equal to about half the maximum width of the greater epithelial ridge, the maximum width of the ridge representing approximately the width of the outspanning zone of the membrane produced upon it.

No other author reports such a high degree of the inward shifting of the organ. I have not studied the pig, but in the rat I get the average distance between the labium vestibulare and the inner edge of the head of the inner pillar cell as follows (table 93).

TABLE 93

Average distance between the labium vestibulare and the inner edge of the inner pillar cell—in μ (albino rat)

AGE	BODY WEIGHT	TURNS OF COCHLEA				
		I	II	III	IV	Average
days	*grams*					
(1) 5	9	94	124	154	165	
(2) 154	102	63	100	134	148	
Difference between age groups 1 and 2		31	24	20	17	23

Therefore, in the rat the organ moves inward on the average of 23 μ; that is, in the ratio of 1:0.16 of the maximum distance between these two points. It may be noted that the difference in this table is not the same in the several turns, but diminishes from base to apex—a relation which is the reverse of that reported by Hardesty ('15) in the pig. I have no explanation for these differences except their possible dependence on the different animals used.

C. On the growth of the largest nerve cells in the ganglion spirale.

Observations. For the present studies the fourteen age groups used in the previous observations on the growth of the tympanic wall of the cochlear duct were employed. In order to see the relation between the growth of the papilla spiralis and the cells of the ganglion spirale, both studies were made on the same sections. In addition, however, I made cross-sections of the cochlea (i.e., at right angles to the axis) in several age groups to follow the growth and the changes in the form of the nerve cells as they appear in this plane. The data for the animals thus used are given in table 94.

For the measurement of the nerve cells a Zeiss system was used with a micrometer eyepiece, having each division equal to 2μ. Since we have in the radial vertical section of the cochlea of the rat at least four turns, there are four cell groups available in each section (fig. 3). The ten largest cells in each ganglion were measured, and thus a total of forty cells in a section were taken for the measurement of the nucleus and the cell.

We used, as stated, four cochleas in each age group, so that 160 cells were measured for each age. Also in the cross-sections the four nearly corresponding turns were used for the measurements, selecting the ten largest cells in each turn.

TABLE 94

Data on rats used for cross-sections of the cochlea—ganglion spirale

AGE	BODY WEIGHT	BODY LENGTH	SEX	SIDE	HEARING
days	*grams*				
15	20	84	♂	L.	Prompt response
20	27	93	♂	L.	" "
25	39	114	♂	L.	" "
100	95	152	♂	R.	" "
150	169	192	♀	L.	" "
371	220	206	♂	L.	" "

In the measurement of the cell bodies the two maximum diameters at right angles to each other were determined, and also the two corresponding diameters for the nuclei.

Here it is to be noted that the expressions turn I, II, III, and IV are used in the same sense as in the earlier chapters.

In table 95 (chart 40) are given the values for the average diameters of the cell bodies and their nuclei in the ganglion spirale in the radial vertical section according to fourteen age groups. Under 'cell body, diameter,' the first column gives the long, the second the short, and the third the computed diameter; i.e., the square root of their products. These last values approximate the mean diameters of the nerve cells. At the foot of the third column are given the ratios from 1 to 20, 1 to 546, and 20 to 546 days. The values for the diameters of the nuclei are similarly given and also the ratios.

As the tables and charts show, the diameters of the cell bodies and also of their nuclei are largest at twenty days of age. After that age they diminish gradually. While the ratio for one to twenty days is 1:1.7 in the cell bodies and 1:1.3 in the nuclei, that for 1 to 546 days is 1:1.6 and 1:1.2, respectively.

TABLE 95

Diameters of the cell bodies and their nuclei in the ganglion spirale (radial-vertical section) (chart 40)

AGE	BODY WEIGHT	BODY LENGTH	Diameters in μ					
			Cell body			Nucleus		
			Long	Short	Computed	Long	Short	Computed
days	*grams*	*mm.*						
1	5	48	11.0	10.0	10.5	8.2	7.6	7.9
3	8	56	12.0	11.1	11.5	8.2	7.8	8.0
6	11	63	13.6	12.3	12.9	8.8	8.1	8.4
9	10	58	14.3	12.8	13.6	8.9	8.2	8.5
12	13	70	14.6	13.1	13.8	8.7	8.2	8.5
15	13	75	15.7	14.1	14.9	9.1	8.4	8.7
20	29	95	19.0	17.3	18.1	10.3	10.0	10.2
25	36	104	18.5	16.9	17.7	10.2	9.9	10.1
50	59	125	18.5	16.6	17.5	10.3	9.7	10.0
100	112	159	18.1	15.7	16.9	9.8	9.2	9.5
150	183	190	18.2	15.3	16.7	9.6	8.8	9.2
257	137	175	18.5	15.3	16.8	9.9	9.4	9.6
366	181	191	18.6	15.3	16.9	9.8	9.0	9.4
546	255	213	18.6	15.3	16.9	9.7	9.0	9.4
Ratios								
1— 20 days					1:1.7			1:1.3
1—546 "					:1.6			:1.2
20—546 "					:0.9			:0.9

In table 96 (chart 41) are a series of computed diameters of the cell bodies and of their nuclei according to the turns of the cochlea. At the bottom of each column are given the ratios from 1 to 20, 1 to 546, and 20 to 546 days. Determining the ratios for each column, it appears that in general the diameters of the cell bodies and their nuclei are largest at twenty days throughout all the turns. This increase is very considerable from fifteen to twenty days. Then they decrease very slowly till 546 days.

Table 97 enables us to compare the ratios in the diameters of the cell bodies and their nuclei in turns I, II, III, and IV in the condensed age groups. In both the cell bodies and their nuclei the ratios become slightly larger in passing from the basal toward the apical turn, except in the one day group, which it reversed.

On the comparison of the diameters of the nerve cell bodies and their nuclei in the ganglion spirale according to sex. For this comparison seven age groups were used. In each age group we have sometimes one, sometimes two cochleas of the same sex.

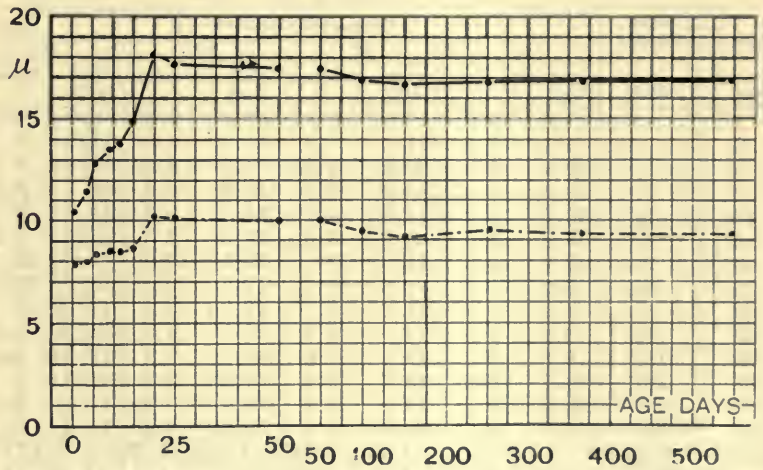

Chart 40 Showing the computed diameter of the largest cell bodies and their nuclei from the ganglion spirale, table 95.

———— Diameters of the cell bodies.

-·-·-·-·- Diameters of the nuclei.

In the latter case the average value is recorded. In table 98 are given the values for these diameters, and it is plain that there is no significant difference in these values according to sex.

On the comparison of the diameters of the nerve cell bodies and their nuclei in the ganglion spirale according to side. For this purpose fourteen age groups were employed. In most cases two cochleas from the same side were used in each age group. In these cases the average value is recorded. Table 99 shows the values for the diameters of the cell bodies and their nuclei according to side, but reveals no evident difference in this character.

On the morphological changes in the ganglion cells during growth. As my sections could not be stained with thionine, my observations on the Nissl bodies are incomplete, yet the slides stained with Heidenhain's iron haematoxylin and van Gieson's stain, as well as by haematoxylin and eosin, were helpful here.

TABLE 96

Computed diameters of the cell bodies and their nuclei in the ganglion spirale according to the turns of the cochlea (chart 41)

AGE	BODY WEIGHT	TURNS OF THE COCHLEA							
		Computed diameters— μ							
		I		II		III		IV	
days	*gms*	Cell body	Nucleus	Cell body	Nucleus	Cell body	Nucleus	Cell body	Nucleus
1	5	11.0	8.0	10.8	8.2	10.4	8.0	9.6	7.4
3	8	11.5	7.9	11.5	7.9	11.7	8.0	11.3	8.1
6	11	12.9	8.4	12.6	8.2	13.0	8.5	13.3	8.6
9	10	13.4	8.4	13.4	8.5	13.6	8.6	13.7	8.6
12	13	13.6	8.1	13.5	8.1	13.8	8.6	14.7	9.0
15	13	14.8	8.6	15.0	8.6	14.6	8.6	15.0	9.2
20	29	17.6	10.0	17.6	9.9	18.1	10.2	19.0	10.4
25	36	16.9	9.9	17.6	10.0	17.6	10.1	18.4	10.3
50	59	17.2	9.7	17.2	9.7	17.6	10.0	17.9	10.1
100	112	16.9	9.6	16.9	9.4	16.3	9.3	16.9	9.6
150	183	16.9	9.3	16.3	9.0	16.6	9.1	17.0	9.1
257	137	16.7	9.6	16.7	9.4	16.9	9.7	17.0	9.7
366	181	16.7	9.3	16.4	9.2	16.7	9.1	17.7	9.7
546	255	15.8	9.2	16.3	9.4	16.9	9.4	17.4	9.5
Ratios 1— 20 days		1:1.6	1:1.3	1:1.6	1:1.2	1:1.7	1:1.3	1:2.0	1:1.4
1—546 "		:1.5	:1.2	:1.5	:1.2	:1.7	:1.2	:1.8	:1.3
20—546 "		:1.0	:0.9	:0.9	:1.0	:0.9	:0.9	:0.9	:0.9

TABLE 97—*Condensed*

Ratios of the diameters of the cells and nuclei of the ganglion spirale

AVERAGE AGE	AVERAGE BODY WEIGHT	RATIOS BETWEEN TURNS					
		I–II		I–III		I–IV	
		Cell body	Nucleus	Cell body	Nucleus	Cell body	Nucleus
days	*grams*						
1	5	1 : 0.98	1:1.25	1:0.95	1:1.00	1 : 0.87	1 : 0.93
8	11	: 0.99	: 1.00	: 1.01	: 1.02	: 1.03	: 1.05
18	21	: 1.01	: 1.00	: 1.01	: 1.01	: 1.04	: 1.05
213	138	: 0.99	: 0.99	: 1.01	: 1.00	: 1.04	: 1.02

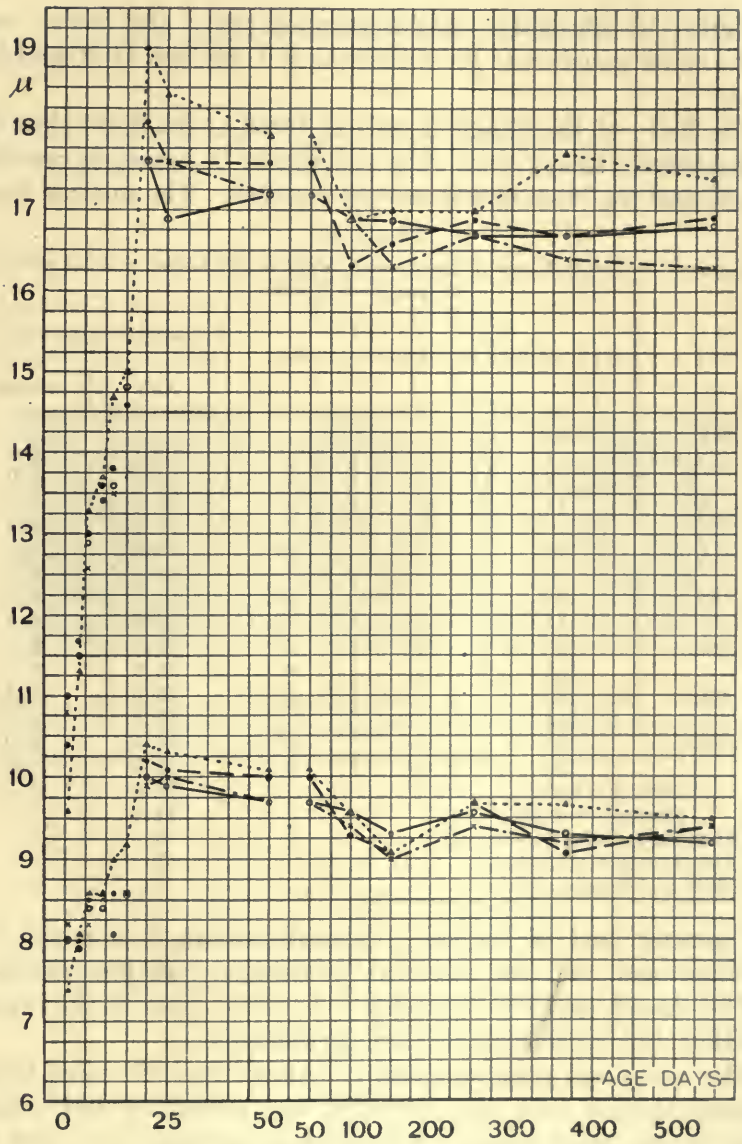

Chart 41 *The computed diameter of the largest cell bodies and of their nuclei from the ganglion spirale, according to the turns of the cochlea, table 96. Upper graphs: diameters of the cell bodies. Lower graphs: diameters of the nuclei of the cells.

Figure 13 illustrates semidiagrammatically the nerve cells in the spiral ganglion of the albino rat at 1 day and at 20 and 366 days.

The body of the ganglion cells at birth is small and has the characteristic fetal form. The cytoplasm is homogeneous and scanty and the Nissl bodies are not yet seen. The nucleus forms

TABLE 98

Comparison according to sex of the diameters of the cell bodies and the nuclei in the ganglion spirale

AGE	BODY WEIGHT	NO. OF RATS	SEX	COMPUTED DIAMETERS— μ	
				Cell	Nucleus
days	*grams*				
3	7	1	♂	11.4	8.0
	8	1	♀	11.4	8.0
6	11	2	♂	13.1	8.5
	10	2	♀	12.8	8.4
9	10	2	♂	13.6	8.5
	9	2	♀	13.5	8.6
12	14	2	♂	13.7	8.5
	12	2	♀	13.9	8.4
100	146	1	♂	17.2	9.6
	103	1	♀	16.9	9.4
150	189	1	♂	16.5	9.1
	154	1	♀	17.1	9.1
365	205	1	♂	16.3	9.0
	170	1	♀	16.7	9.1
Average—male				14.5	8.7
Average—female				14.6	8.7
Male larger than female				3	3
Female larger than male				3	2
Male and female equal				1	2

the greater part of the cell. The chromatin is not yet well differentiated, and the so-called 'Kernfaden' are not visible.

The sharply marked nucleolus is in most cases in the central position, but sometimes located peripherally.

The cytoplasm matures rapidly. At six days the Nissl bodies appear, though they are of course, less abundant and smaller than in the later stages. The nucleus develops also and the chromatin is well differentiated. Thus the development in both the cell body and the nucleus proceeds rapidly in the earlier stage.

Fig. 13 Showing semi-diagrammatically the size and the morphological changes in the ganglion cells in the ganglion spirale of the albino rat at the age of 1, 20 and 366 days. All cell figures have been uniformly magnified 1000 diameters.

At twenty days the cell body reaches its maximum size. The Nissl bodies are large and abundant. The nucleus also attains

TABLE 99

Comparison according to side of the cell bodies and their nuclei in the ganglion spirale

AGE	BODY WEIGHT	NO. OF RATS	SIDE	COMPUTED DIAMETERS— μ	
				Cell	Nucleus
days	*grams*				
1	5	2	R.	10.6	8.0
			L.	10.4	7.8
3	7	1	R.	11.4	8.0
			L.	11.5	8.0
6	11	2	R.	13.0	8.5
			L.	12.9	8.4
9	9	2	R.	13.4	8.5
			L.	13.7	8.6
12	12	1	R.	13.9	8.4
			L.	14.0	8.4
15	13	1	R.	14.7	8.6
			L.	14.8	8.5
20	29	2	R.	18.0	10.1
			L.	18.5	10.2
25	36	2	R.	17.6	10.1
			L.	17.7	10.1
50	59	2	R.	17.5	9.9
			L.	17.5	9.8
100	102	2	R.	16.8	9.5
	123		L.	17.0	9.5
150	189	1	R.	16.4	9.2
			L.	16.5	9.1
257	137	2	R.	17.1	9.7
			L.	16.6	9.5
367	175	2	R.	17.3	9.7
365	188		L.	16.5	9.1
546	255	2	R.	16.9	9.3
			L.	16.9	9.3
Average right side				15.3	9.1
Average left side				15.3	9.0
Right larger than left				4	7
Left larger than right				8	2
Right and left equal				2	5

its maximum size at this age, though the rate of increase is slower than that for the cell body. With this increase of size the histological structure becomes that of the adult rat. Then, as the

age advances, the size of both the cell body and of the nucleus slowly diminishes, while within the cytoplasm the differentiation of the Nissl bodies progresses. This relation is seen in the figure of the cell at 366 days, which shows that the absolute volume of the cell body and also of the nucleus is smaller than at twenty days.

From twenty to 366 days, gradual and progressive changes in all histological structures can be seen, though there are no sudden changes.

TABLE 100

Diameters of the cell bodies and their nuclei in the ganglion spirale—in cross sections of the cochlea (chart 42)

AGE	BODY WEIGHT	DIAMETERS IN μ					
		Cell body			Nucleus		
		Long	Short	Computed	Long	Short	Computed
days	*grams*						
15	20	15.7	14.3	15.0	9.3	8.4	8.8
20	27	18.3	16.6	17.4	10.3	10.0	10.1
25	39	18.0	16.6	17.3	10.1	9.8	9.9
100	95	17.6	16.2	16.9	9.9	9.5	9.7
150	169	17.4	16.0	16.7	9.8	9.1	9.4
371	220	16.5	15.8	16.2	9.5	8.6	9.0
Ratios 15— 25 days				1 : 1.1			1 : 1.1
15—371 "				: 1.1			: 1.0
25—371 "				: 1.0			: 0.9

The question here arose whether this change in volume was in any way related to a shift in the long axis of the cell at the later ages. To answer this difficult question it was deemed desirable to compare the form of the ganglion cells obtained in the cross-section with that found in the radial section of the cochlea. In table 100 (chart 42) are given the values for the diameters of the cell bodies and their nuclei in the ganglion spirale in the cross-section. Below are given the respective ratios from 15 to 25, 15 to 371, and 25 to 371 days. Both cell body and nucleus increase in size up to twenty days and then diminish very slowly, as the age advances. These are similar to the relations found in the radial sections.

Looking at the diameters of the cell bodies and their nuclei in each turn (table 101), we do not find in the later age groups a regular increase in passing from the base toward the apex, as in the cells on the radial section. The differences are generally

TABLE 101

Diameter of the cell bodies and their nuclei in the ganglion spirale according to the turns of the cochlea (cross section)

AGE	BODY WEIGHT		TURNS OF THE COCHLEA							
			I		II		III		IV	
			Computed diameters— μ							
		Cell body	Nucleus	Cell body	Nucleus	Cell body	Nucleus	Cell body	Nucleus	
days	*grams*									
15	20	15.0	8.7	14.7	8.8	14.9	8.9	14.9	9.0	
20	27	16.7	9.7	17.2	10.0	17.5	10.1	18.1	10.6	
25	39	16.9	10.0	17.2	9.9	17.6	9.8	17.3	10.0	
100	95	17.2	10.0	16.9	9.6	16.7	9.6	16.8	9.6	
150	169	17.0	9.9	16.6	9.3	16.6	9.4	16.4	9.1	
371	220	16.2	9.6	16.2	9.1	16.0	8.7	16.3	9.0	
Ratio 15–371 days		1:1.1	1:1.1	1:1.1	1:1.0	1:1.1	1:1.0	1:1.1	1:1.0	

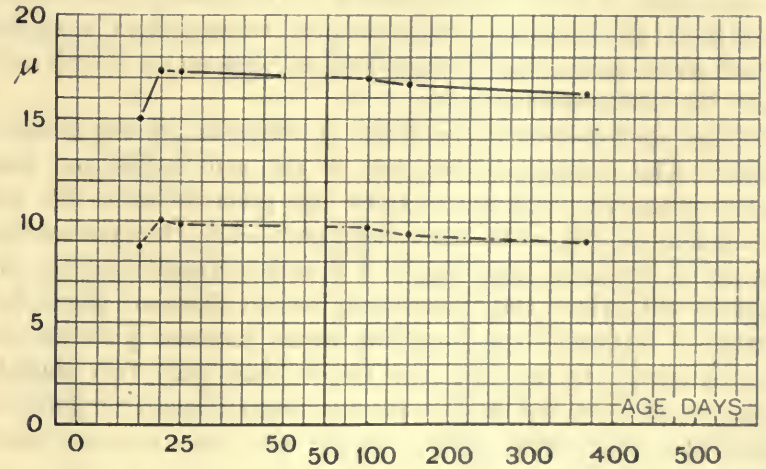

Chart 42 The average diameter of the largest cell bodies and of their nuclei of the nerve cells from the ganglion spirale, after 15 days (cross-section), table 100.

———— Cell bodies. -.-.-.-.-. Nuclei.

far smaller than on the radial section. This result seems to have some connection with the position of the long axis of the ganglion cells in relation to the axis of the cochlea.

Comparing the diameters of the cell bodies and their nuclei in nearly corresponding places in the radial and cross-section, the long diameters of the cells are in each age group almost always larger in the radial than on the cross-section. Therefore the cells are somewhat ovoid. The short diameters, however, are at the same age sometimes longer, sometimes shorter on the radial than on the cross-section. This is probably due to the fact that in the upper turns the cells stand with their long diameter more nearly parallel to the axis of the modiolus, and therefore, on passing from the upper to the lower turn, the long axes of the cells become more inclined to the modiolus.

In order to show that the cell form is ovoid, I reconstructed the cells at 15, 100, and 365 days of age by the usual method, and obtained models which agreed in form with that determined by the microscope.

It appears, therefore, that while there is some difference in the diameters of these cells according to the plane of the section, neverthless, the change in volume after twenty days is similar in both cases, and so this change does not depend on the plane in which the sections were made.

On the nucleus-plasma relations of the cells in the ganglion spirale. The computed diameters of the cell bodies and their nuclei, measured on radial sections, are given in table 102 and the nucleus-plasma ratios have been entered in the last column. The ratio is at one day only 1:1.3 and increases rapidly and regularly till twenty days; after that period there are slight fluctuations. Generally speaking, the ratios increase with the advancing age of the rat, but after twenty days only very slightly. Thus we see that the nucleus-plasma relation nearly reaches an equilibrium at twenty days, though the cells mature slowly even after that time.

When we consider this relation according to the turns of the cochlea, we find that this ratio increases in all the turns regularly and definitely till twenty days, after which there are some

fluctuations (table 103). Thus we see here also the same relation as before.

TABLE 102

Nucleus-plasma ratios of cells in the ganglion spirale (radial-vertical section)

AGE	BODY WEIGHT	BODY LENGTH	COMPUTED DIAMETERS— μ		
			Cell body	Nucleus	Nucleus-plasma ratios
days	*grams*	*mm.*			
1	5	48	10.5	7.9	1 : 1.3
3	8	56	11.5	8.0	: 2.0
6	11	63	12.9	8.4	: 2.6
9	10	58	13.6	8.5	: 3.1
12	13	60	13.8	8.5	: 3.3
15	13	75	14.9	8.7	: 4.0
20	29	95	18.1	10.2	: 4.6
25	36	104	17.7	10.1	: 4.4
50	59	125	17.5	10.0	: 4.4
100	112	159	16.9	9.5	: 4.6
150	183	190	16.7	9.2	: 5.0
257	137	175	16.8	9.6	: 4.4
366	181	191	16.9	9.4	: 4.8
546	255	213	16.9	9.4	: 4.8

TABLE 103

Nucleus-plasma ratios of cells in the ganglion spirale according to the turns of the cochlea. Based on table 96

AGE	BODY WEIGHT	TURNS OF THE COCHLEA			
		I	II	III	IV
days	*grams*				
1	5	1 : 1.6	1 : 1.5	1 : 1.2	1 : 1.2
3	8	: 2.1	: 2.1	: 2.1	: 1.7
6	11	: 2.6	: 2.6	: 2.6	: 2.7
9	10	: 3.1	: 2.9	: 3.0	: 3.0
12	13	: 3.7	: 3.6	: 3.1	: 3.4
15	13	: 4.1	: 4.3	: 3.9	: 3.2
20	29	: 4.5	: 4.6	: 4.6	: 5.1
25	36	: 4.0	: 4.5	: 4.3	: 4.7
50	59	: 4.6	: 4.6	: 4.5	: 4.6
100	112	: 4.5	: 4.8	: 4.4	: 4.5
150	183	: 5.0	: 4.9	: 5.1	: 5.5
257	137	: 4.3	: 4.6	: 4.3	: 4.4
366	181	: 4.8	: 4.7	: 5.2	: 5.1
546	255	: 5.1	: 4.2	: 4.8	: 5.1

In the nucleus-plasma ratio of the cells on the cross-section, as shown in table 104, the increase with age is very regular. As the diameters of the cell bodies and their nuclei decrease slowly after twenty days, this increase of the ratio means that the nuclei are diminishing relatively more rapidly than the cytoplasm.

Comparing these ratios from the radial and cross sections, we find that they agree (table 105).

TABLE 104

Nucleus-plasma ratios of the cells in the ganglion spirale (cross-sections)

AGE	BODY WEIGHT	BODY LENGTH	COMPUTED DIAMETERS— μ		
			Cell body	Nucleus	Nucleus-plasma ratios
days	*grams*	*mm.*			
15	20	84	15.0	8.8	1 : 4.0
20	27	93	17.4	10.1	: 4.1
25	39	114	17.3	9.9	: 4.3
100	95	152	16.9	9.7	: 4.5
150	169	192	16.7	9.4	: 4.6
371	220	206	16.2	9.0	: 4.8

TABLE 105

The nucleus-plasma ratios according to the plane of the section at two age periods— albino rat

AGE	NUCLEUS-PLASMA RATIO ON THE RADIAL SECTION	NUCLEUS-PLASMA RATIO ON THE CROSS SECTION	AGE
days			*days*
15	1 : 4.0	1 : 4.0	15
366	1 : 4.8	1 : 4.8	371

Discussion. According to the foregoing data, the maximum size of the cells in the ganglion spirale, at twenty days, is in cross-sections about 18.7 × 16.9 μ for the cell body and 10.3 × 10.0 μ for the nucleus. Both the long and short diameter of the cell body thus obtained is therefore a little less than that obtained in the radial section, while the diameters for the nucleus are the same.

In the literature we have not found any data for the Norway rat, but there are a few observations on the size of these cells in other mammals by Kölliker ('67) and von Ebner ('02).

Schwalbe ('87) and Alagna ('09) find these ganglion cells 25 to 30 μ in diameter in the guniea-pig and cat.

Alexander ('99) has also reported measurements on a series of mammals, but as the size of such cells is greatly influenced by the method of preparation, and as our averages are based on *the largest cells* while those of other authors have been obtained in a different manner, it seems best not to report the other values in the literature, as they are sure to be misleading.

TABLE 106

Showing the changes with age in the diameters of the cells and the nuclei of the spiral ganglion and the lamina pyrmidalis of the cerebral cortex, respectively

AGE	CELL BODY IN THE GANGL. SPIRALE COMPUTED DIAM. μ	CELL BODY IN THE LAMINA PYRAMID COMPUTED DIAM.	NUCLEUS IN GANGL. SPIR. COMP. DIAM.	NUCLEUS IN THE LAMINA PYRAM. COMP. DIAM.	AGE
days					*days*
1	10.5	11.4	7.9	9.4	1
20	18.1	18.7	10.2	15.7	20
546	16.9	17.0	9.4	13.8	730
Ratio between 1 and 20 days	1 : 1.7	1 : 1.6	1 : 1.3	1 : 1.3	ratio of 1 to 20 days
Ratio between 1 and 546 days	1 : 1.6	1 : 1.5	1 : 1.2	1 : 1.2	ratio of 1 to 730 days

Considering the course of growth in these cells, we find it to be similar in both the spiral ganglion and the lamina pyramidalis of the cerebral cortex (rat) as reported by Sugita ('18). In the former the cells attain at twenty days of age, the time of weaning, their maximum size, and then diminish slowly with advancing age. The cells of the lamina pyramidalis also reach their full size at twenty days, and then diminish in the same way. Therefore, the course of the growth of both of these groups of nerve cells coincides. However, I do not know of other instances of the phenomenon. When tabulated, the relations here noted appear as in table 106.

The difference between them is only in the absolute values of the diameters of the cell bodies and especially of the nuclei,

the nuclei in the cells of the lamina pyramidalis being decidedly larger than in those of the spiral ganglion. The ratios of increase are, however, similar.

When we consider the increasing ratios of the diameters of the ganglion cells, we see a close similarity in the maximum values between the cells in the spiral and gasserian ganglion (Nittono, '20). Nevertheless while in the former the ratios from 1 to 20 and 1 to 366 days are in the cell bodies 1: 1.7 and 1: 1.6, respectively, in the latter the ratios for the corresponding intervals are 1: 1.43 and 1: 1.69, respectively (Nittono, '20, p. 235). In the nucleus also similar relations are to be seen in both ganglia.

As these ratios show, there is in the gasserian ganglion a definite increase in the diameters of cells and nuclei after 20 days of age; the time when the maximum is reached by the cells of the spiral ganglion. Thus the former continue to grow after growth in the latter has ceased. These results suggest that the neurons in the more specialized ganglia, like the spiral ganglion, may mature earlier than do those in the less specialized.

On the correlation between the growth of the hair cells of the papilla spiralis and of the nerve cells of the ganglion spirale. When we compare the growth changes in the hair cells with those in the ganglion cells, we find that the course of the development is similar. Both classes increase in volume from one to twenty days of age, then tend to diminish slowly—the hair cells more slowly than the ganglion cells. In the ratios of increase, however, there are marked differences. Thus in table 67 (bottom of last column) the volume ratios from 1 to 20 and 20 to 546 days are 1: 2.4 and 1: 0.9, respectively in the hair cells, and in the ganglion cells, table 108, the ratios of the volumes in the fourth column work out for the corresponding ages as 1: 5.1 and 1: 0.8, respectively. In the case of the nuclei the growth changes are somewhat different. In the hair cells the nucleus grows in diameter more rapidly, and therefore reaches at nine days its maximum value and then diminishes at succeeding ages.

I have sought to determine whether there was any correlation in growth between either the entire cylindrical surface or the area of the cross-section of the hair cells, on the one hand and the volume

of the cells of the ganglion spirale on the other. The reason for making this comparison was the fact that Levi ('08), Busacca ('16), and Donaldson and Nagasaka ('18) have noted in the cells of the spinal ganglia of several mammals that the postnatal growth in volume was correlated with the increase in the area of the body surface, and recently Nittono ('20) has found in the rat a similar relation between the growth of the cells of the gasserian ganglion and the area of the skin of the head. On examining this problem, it is evident that the correlations thus far reported

TABLE 107

Comparison of ratios between the volumes of the cells of the ganglion spirale and the ratios of the area of the cylindrical surface of the hair cells of the organ of Corti—on the maximum values

AGE	BODY WEIGHT	VOLUME OF THE GANGLION CELL μ^3	RATIOS ON THE MAXIMUM VALUE	AREA OF CYLINDRICAL SURFACE OF THE HAIR CELLS μ^2	RATIOS ON THE MAXIMUM VALUE
days	*gms.*				
1	5	606 : 3105	1 : 5.12	395 : 723	1 : 1.83
3	8	796 : "	: 3.90	463 : "	: 1.56
6	11	1124 : "	: 2.76	582 : "	: 1.24
9	10	1317 : "	: 2.36	648 : "	: 1.12
12	13	1376 : "	: 2.26	681 : "	: 1.03
15	13	1732 : "	: 1.79	729 : "	: 0.99
20	29	3105 : "	: 1.00	723 : "	: 1.00
25	36	2903 : "	: 1.07	691 : "	: 1.05
50	59	2806 : "	: 1.11	697 : "	: 1.04
100	112	2527 : "	: 1.23	678 : "	: 1.07
150	183	2439 : "	: 1.28	691 : "	: 1.05
257	137	2483 : "	: 1.25	689 : "	: 1.05
366	181	2527 : "	: 1.23	683 : "	: 1.06
546	255	2527 : "	: 1.23	699 : "	: 1.03

apply to the postnatal growth period, and that we must consider that the functional relations of the skin are well established, even at the earliest age. The data with which we have worked in the case of the cochlea are presented in several tables (107 to 110).

In tables 107 and 108 are given the volumes of the cells of the ganglion spirale and the areas of the cylindrical surface of the hair cells. In table 107 the ratios are computed by dividing the maximum value by the values at each age, and in table 108 by dividing the values at each age by the initial value.

TABLE 108

Comparison of the ratios of the volume of the cells of the ganglion spirale with the ratios of the area of the cylindrical surface of the hair cells of the organ of Corti—on the initial values

AGE	BODY WEIGHT	VOLUME OF THE GANGLION CELLS— μ^3	RATIOS ON THE INITIAL VALUE	AREA OF THE CYLINDRICAL SURFACE OF THE HAIR CELLS— μ^2	RATIOS ON THE INITIAL VALUE
days	*grams*				
1	5	606 : 606 : :	1 : 1.00	395 : 395 : :	1 : 1.00
3	8	: 796 : :	: 1.31	: 463 : :	: 1.17
6	11	: 1124 : :	: 1.85	: 582 : :	: 1.47
9	10	: 1317 : :	: 2.17	: 648 : :	: 1.64
12	13	: 1376 : :	: 2.27	: 681 : :	: 1.72
15	13	: 1732 : :	: 2.86	: 729 : :	: 1.85
20	29	: 3105 : :	: 5.12	: 723 : :	: 1.83
25	36	: 2903 : :	: 4.79	: 691 : :	: 1.75
50	59	: 2806 : :	: 4.63	: 697 : :	: 1.76
100	112	: 2527 : :	: 4.17	: 678 : :	: 1.72
150	183	: 2439 : :	: 4.02	: 691 : :	: 1.75
257	137	: 2483 : :	: 4.10	: 689 : :	: 1.74
366	181	: 2527 : :	: 4.17	: 683 : :	: 1.73
546	255	: 2527 : :	: 4.17	: 699 : :	: 1.77

TABLE 109

Area of the cross-section of the inner and outer hair cells

AGE	BODY WEIGHT	DIAMETER OF ONE INNER HAIR CELL μ	AVERAGE DIAMETER OF THREE OUTER HAIR CELLS μ	WEIGHTED DIAMETER OF INNER AND OUTER HAIR CELLS μ	WEIGHTED AREAS OF CROSS SECTION OF HAIR CELLS μ^2
days	*grams*				
1	5	6.6	6.0	6.2	30
3	8	8.0	7.4	7.6	45
6	11	8.1	7.6	7.7	48
9	10	8.8	8.5	8.6	58
12	13	8.5	8.3	8.4	55
15	13	8.4	7.7	7.9	50
20	29	8.8	8.2	8.4	55
25	36	8.8	8.1	8.3	55
50	59	8.8	8.2	8.4	55
100	112	8.6	8.1	8.2	53
150	183	8.5	8.3	8.4	55
257	137	8.5	8.3	8.4	55
366	181	8.8	8.4	8.5	58
546	255	8.6	8.2	8.3	55

I have calculated the cylindrical surface of the hair cells according to the formula for the lateral surface of a cylinder; therefore, this area equals $2 \pi r a$ (r = radius, a = height of the cylinder). As the hair cells are more or less pointed at their lower end, the surface obtained by this formula has nearly the value of the total surface of the hair cells less that for the upper end disk.

As has been already shown, both classes of cells grow rapidly from birth to twenty days, and after that both tend to decrease slightly in volume. It is evident that during the growing period,

TABLE 110

Comparison of the ratios of the volume of the cells of the ganglion spirale with the ratios of the areas of the cross-section of the inner and outer hair cells of the organ of Corti

AGE *days*	BODY WEIGHT *gms*	VOLUME OF THE GANGLION CELLS— μ^3	RATIOS ON THE INITIAL VALUE	AREA OF THE CROSS-SECTION OF THE HAIR CELLS	RATIOS ON THE INITIAL VALUE
1	5	606 : 606	1 : 1.00	30 : 30	1 : 1.00
3	8	: 796	: 1.31	: 45	: 1.50
6	11	: 1124	: 1.85	: 48	: 1.60
9	10	: 1317	: 2.17	: 58	: 1.93
12	13	: 1376	: 2.27	: 55	: 1.83
15	13	: 1732	: 2.86	: 50	: 1.67
20	29	: 3105	: 5.12	: 55	: 1.83
25	36	: 2903	: 4.79	: 55	: 1.83
50	59	: 2806	: 4.63	:53	: 1.77
100	112	: 2527	: 4.17	: 53	: 1.77
150	183	: 2439	: 4.02	: 55	: 1.83
257	137	: 2483	: 4.10	: 55	: 1.83
366	181	: 2527	: 4.17	: 58	: 1.93
546	255	: 2527	: 4.17	: 55	: 1.83

from one day to the end of the record, the volumes of the ganglion cells increase more rapidly than do the cylindrical areas of the hair cells (table 108). If we seek a numerical expression of these relations, it seems best to start not with the values at birth, but with those at nine days of age when the cochlea is just beginning to function, and to extend the comparison only up to twenty days when both groups of cells have reached their maximum size.

Thus at nine days (table 108) the volume of the ganglion cells is 1317 μ^3, while at twenty days it is 3105 μ^3, or as 1: 2.3, while the area of the cylindrical surfaces of the hair cells at the respective

ages is 648 μ^3 and 723 μ^3, or as 1:1.1, thus showing a rapid growth of the ganglion cell bodies accompanied by but slight enlargement of the hair cells.

It is evident from these ratios that the ganglion cells are increasing in volume more rapidly than the hair cells in area. It is possible that the nervus cochlearis innervates the other cells of the cochlea as well, but even if this is taken into consideration the general relations remain the same.

It follows from this that during the period between the earliest appearance of the functional response (nine days) and the attainment of the maximum size of the cells, the innervation of the hair cells is steadily improving, if we may infer such an improvement from the increase in the volume of the ganglion cells. After the close of this early growing period the relations are approximately fixed through the remainder of life. We do not find, therefore, in the cochlea any relation which corresponds to those found between the spinal ganglion cells or those of the gasserian ganglion and the associated areas of the skin during postnatal growth. This seems to indicate that in the cochlea growth is fixed or limited, while in the body as a whole it is more or less continuous, and the ganglion cells behave differently in the two cases.

In table 109 are shown the diameters of the inner and outer hair cells and their weighted diameters. In the last column is given the area of the cross-section of the hair cells.

The ratios of these areas on the initial area are shown in table 110 in comparison with the volumes of the ganglion cells on the initial volume, and indicate that from three days of age the values for the ganglion cells are increasing more rapidly than those for the area of the cross-section of the hair cells, and at twenty days the increase in the case of both elements has reached a maximum. Here, as in the case of the cylindrical surface, both elements show like phases of growth, but the increase in the volumes of the ganglion cells is much greater than the increase in the cylindrical area or cross-section of the hair cells.

As it may be desirable to use for comparison the measurements on the cells of the ganglion spirale as here reported, the

constants for the determinations based on 160 cells in each age group are given in table 111 for the radial vertical sections and in table 112 for the cross-sections.

TABLE 111

Analytical constants[6] giving the mean, standard deviation and coefficient of variability with their respective probable errors for the diameters of the cells and their nuclei of the ganglion spirale in radial vertical section

AGE *days*	FOR TOTAL NUMBER OF CELLS			
	Cell Nucleus	Mean	Standard deviation	Coefficient of variability
1	Cell	10.2 ± 0.05	0.90 ± 0.03	8.9 ± 0.33
	Nucleus	7.8 ± 0.02	0.46 ± 0.01	5.9 ± 0.22
3	Cell	11.3 ± 0.03	0.50 ± 0.02	4.4 ± 0.17
	Nucleus	7.9 ± 0.02	0.32 ± 0.01	4.1 ± 0.15
6	Cell	12.6 ± 0.04	0.68 ± 0.03	5.4 ± 0.20
	Nucleus	8.4 ± 0.03	0.48 ± 0.02	5.7 ± 0.22
9	Cell	13.1 ± 0.03	0.61 ± 0.02	4.7 ± 0.18
	Nucleus	8.5 ± 0.03	0.52 ± 0.02	6.1 ± 0.23
12	Cell	13.4 ± 0.05	0.86 ± 0.03	6.4 ± 0.24
	Nucleus	8.4 ± 0.03	0.61 ± 0.02	7.3 ± 0.28
15	Cell	14.6 ± 0.04	0.73 ± 0.03	5.0 ± 0.13
	Nucleus	8.7 ± 0.03	0.58 ± 0.02	6.7 ± 0.25
20	Cell	17.8 ± 0.06	1.17 ± 0.04	6.6 ± 0.25
	Nucleus	10.0 ± 0.02	0.40 ± 0.02	4.1 ± 0.15
25	Cell	17.3 ± 0.05	0.88 ± 0.03	5.1 ± 0.19
	Nucleus	9.9 ± 0.02	0.36 ± 0.01	3.6 ± 0.14
50	Cell	17.2 ± 0.04	0.78 ± 0.03	4.5 ± 0.17
	Nucleus	9.7 ± 0.02	0.34 ± 0.01	3.6 ± 0.14
100	Cell	16.5 ± 0.03	0.65 ± 0.02	3.9 ± 0.15
	Nucleus	9.4 ± 0.02	0.38 ± 0.01	4.0 ± 0.15
150	Cell	16.4 ± 0.03	0.79 ± 0.02	4.8 ± 0.18
	Nucleus	9.1 ± 0.02	0.42 ± 0.02	4.6 ± 0.17
257	Cell	16.6 ± 0.06	1.09 ± 0.04	6.6 ± 0.25
	Nucleus	9.5 ± 0.02	0.39 ± 0.01	4.1 ± 0.15
366	Cell	16.7 ± 0.05	1.02 ± 0.01	6.1 ± 0.22
	Nucleus	9.3 ± 0.03	0.52 ± 0.02	5.6 ± 0.21
546	Cell	16.7 ± 0.06	1.06 ± 0.04	6.4 ± 0.24
	Nucleus	9.3 ± 0.02	0.45 ± 0.02	4.9 ± 0.18

Conclusion. For the study of the growth of the nerve cells in the ganglion spirale fourteen age groups were taken and the data obtained from the 160 largest cells in each age group. Besides these, six age groups, representing six cochleas, were examined in cross-sections to determine the form of the ganglion

cells and the relation of their long axes to the axis of the cochlea. Here also the ten largest cells in each of four, nearly corresponding turns, were measured. We obtained the following results:

1. As thus prepared, the ganglion cells at birth have a maximum size of 11 × 10 μ in cell body and 8.2 × 7.6 μ in nucleus. At twenty days the diameters are the largest, 18.7 × 16.9 μ in cell body and 10.3 × 10.0 μ in nucleus.

TABLE 112

Analytical constants giving the mean, standard deviation and coefficient of variability with their respective probable errors for the diameters of the cells and their nuclei of the ganglion spirale, in cross-section

AGE	Cell Nucleus	FOR TOTAL NUMBER OF CELLS		
		Mean	Standard deviation	Coefficient of variability
days				
15	Cell	14.7 ± 0.04	0.40 ± 0.03	2.7 ± 0.21
	Nucleus	8.9 ± 0.04	0.34 ± 0.03	3.8 ± 0.29
20	Cell	17.1 ± 0.09	0.83 ± 0.06	4.9 ± 0.37
	Nucleus	10.0 ± 0.06	0.58 ± 0.04	5.8 ± 0.44
25	Cell	17.1 ± 0.07	0.63 ± 0.05	3.7 ± 0.28
	Nucleus	9.8 ± 0.03	0.30 ± 0.02	3.1 ± 0.23
100	Cell	16.7 ± 0.05	0.44 ± 0.03	2.6 ± 0.20
	Nucleus	9.6 ± 0.04	0.36 ± 0.03	3.7 ± 0.25
150	Cell	16.4 ± 0.07	0.69 ± 0.05	4.2 ± 0.32
	Nucleus	9.4 ± 0.05	0.46 ± 0.03	4.9 ± 0.37
371	Cell	16.0 ± 0.06	0.55 ± 0.04	3.5 ± 0.24
	Nucleus	9.1 ± 0.05	0.43 ± 0.03	4.7 ± 0.36

2. The ganglion cells grow relatively rapidly after birth and reach at twenty days of age their maximum size. After having passed the maximum at twenty days, they diminish in size very slowly, but the internal structure matures more and more with successive age.

3. The nuclei are relatively large at birth but increase more slowly than the cell bodies do; nevertheless, they follow the same course of development as the latter. This peculiar course in the growth of the ganglion cells is similar to that followed by the cells of the lamina pyramidalis of the cerebral cortex of the rat as found by Sugita ('18).

4. Within the cochlea the cell bodies and nuclei increase their diameters from the base toward the apex, except in the earlier stages.

5. There are no evident differences in the diameters of the cell bodies and the nuclei of the ganglion cells either according to sex or side.

6. Both the cell bodies and the nuclei are immature at birth, but differentiate rapidly, and even at six days the Nissl bodies are visible. The differentiation proceeds with advancing age.

7. The ganglion cells are bipolar and oval in shape. The direction of the long axis of the cells differs according to the turn of the cochlea and in the upper turn it runs almost parallel to the axis of the modiolus but inclines more and more to the horizontal position on passing to the base.

8. The nucleus-plasma ratios of the ganglion cells increase with age in both the radial and cross-sections.

9. The increase in the volume of the ganglion cells and the area of the cross-section of the hair cells is approximately similar during the first nine days of life, but after that the ganglion cells increase relatively very rapidly. These relations are very different from those found for the spinal ganglion cells by Donaldson and Nagasaka ('18) and for the cells of the gasserian ganglion by Nittono ('20).

The nervus cochlearis innervates not only the hair cells, but all the elements of the cochlea, and this may have some influence upon this relation. It is interesting to note that the rate of increase in the cylindrical surface of the hair cells is similar to that in the area of the cross-sections of these same cells.

II. CORRELATION BETWEEN THE INCEPTION OF HEARING AND THE GROWTH OF THE COCHLEA

The present study aims merely to compare in the rat the size of each element of the cochlea just before and just after the appearance of hearing and to ascertain the changes in the cochlea which take place during this phase. The rats which have sense of hearing show the so-called 'Ohrmuschelreflex'

of Preyer and other responses to auditory tests. Both the guinea-pig and rat react most evidently to sounds. The former animal responds usually five to six hours after birth. In the rat, however, the development of the function is, as already stated, relatively retarded and usually first appears at about ten days of age.

To test the presence of hearing there are several methods, as for example, Preyer's' Ohrmuschelreflex' and the reflex closure of the eyelid, and these I used in making my observations. As the source of the sound I selected the hand clap, a whistle (Triller-pfeife, about c^4) and a low sound made by drawing in the breadth with nearly closed lips (about c^1).

Since it is my purpose merely to determine the first appearance of a response to sound, it is not nescessary to carry out such refined examinations as did Hunter ('14, '15, '18) Watson ('07), and others on white rats, and Marx ('09) on the guinea-pig, nor was it necessary to use the tuning-fork which by the way is not so good for tests on animals as for those on man. Since sometimes we may have a defect of hearing in animals, as shown by many investigators, it was deemed necessary to use several sources of sound and to take care not to produce air currents striking the test animal or to touch it in any way. For this purpose a large sheet of glass was placed between the source of sound and the rats to be tested. While the rat was resting I suddenly produced the sound and noted whether the rat responded. When the animals already had their eyes open the test was made from behind to avoid visual reflexes.

Observations

Rats at birth show no response to auditory stimuli. Most of them respond at twelve days of age very clearly, sometimes at ten to eleven days Under certain circumstances, the time of the reflex can be rather accurately noted. For example, while in the morning at ten days no reflex was noted it was present in the evening of the same day. Fortunately, I obtained five nine-day-old rats belonging to one litter and in nearly the same condition of nourishment and developnent. One of these

responded to the test very evidently at noon on the ninth day, but the others did not. The sound which was effective was fairly intense, but to a faint and low-pitched sound this rat did not respond. In this case the external auditory canal was open. In the others there was in some a small open canal, but more or less closed by a cellular plug. In the latter cases I removed this obstruction without much difficulty or damage by washing, yet no reaction could be obtained to the stimuli. As it was to be expected, that also in the latter the reflexes would very shortly appear, all the cochleas of these young rats, both the not-hearing and hearing, were fixed by the method previously described and later examined.

In chapter 1, in which I followed the growth changes in the constituents of the membranous cochlea and in its ganglion cells from birth to maturity, including 'not hearing' and 'hearing' rats, very evident differences were observed in rats between nine and twelve days of age. In view of this, it will be of interest to compare the measurements obtained from the 'not hearing' and 'hearing' rats nine days old and members of the same litter. From the differences thus obtained we can conclude concerning the developmental changes in the cochlea requisite for the first appearance of hearing, provided there are no obstacles in the sound-conducting apparatus or deficiencies in the central organ.

In table 113 are given the values for the size of the several constituents of the cochlea from a rat which did not hear and one which did, at nine days. The former data are the averages from four cochleas, while the latter are from two. The table shows in a striking way that where there is a significant difference. The values obtained from the rat which could hear are usually larger than those of the rat which could not hear.

Among these measurements we see sometimes very marked and sometimes only slight differences. Only the radial distance between the labium vestibulare and the inner edge of the head of the inner pillar cell in the first two turns and the diameter of the nuclei of the inner and outer hair cells are in the former smaller than in the latter. In both instances, however, these smaller

TABLE 113

Comparison of the dimensions of the constituents of the cochlea in a hearing rat (H.) with those in a rat not hearing (N.) at nine days of age—measurements in micra

RAT	AGE	BODY WEIGHT
	days	*grams*
(N.)	9	10
(H.)	9	11

	Average distance between two spiral ligaments
(N.)	1430
(H.)	1434

Breadth of membrana tectoria

	TURN I	II	III	IV	Average		Th ickness
(N.)	243	270	304	306	281		27
(H.)	242	268	308	314	283		27

Breadth of membrana basilaris

	TURN I	II	III	IV	AVERAGE	ZONA ARCUATA	ZONA PECTINATA
(N.)	169	189	202	201	191	79	112
(H.)	171	186	214	204	196	93	103

Distance between the habenula perforata and the outer corner of the inner hair cell

	TURN I	II	III	IV	AVERAGE
(N.)	38	38	44	49	42
(H.)	40	42	58	60	50

Distance between habenula perforata and the outer corner of the outer pillar cell at foot

	TURN I	II	III	IV	Average
(N.)	70	76	86	86	79
(H.)	79	88	103	102	93

Height of greater epithelial ridge

	TURN I	II	III	IV	AVERAGE
(N.)	36	40	41	42	40
(H.)	42	43	48	50	46

Distance between the labium vestibulare and the habenula perforata

	TURN I	II	III	IV	Average
(N.)	83	108	137	145	118
(H.)	85	104	140	150	120

TABLE 113—*Continued*

Distance between the labium vestibulare and the inner edge of the head of the inner pillar cell

	TURN I	II	III	IV	Average
(N.)	94	131	168	179	143
(H.)	78	108	170	210	142

Height from basal plane to surface of pillar cells

	TURN I	II	III	IV	AVERAGE
(N.)	32	33	35	36	34
(H.)	40	42	45	45	43

Height of tunnel of Corti

	TURN I	II	III	IV	AVERAGE
(N.)	0	0	0	0	0
(H.)	20	18	14	11	16

Height of papilla spiralis at the third series of outer hair cells

	TURN I	II	III	IV	AVERAGE
(N.)	28	28	27	28	28
(H.)	42	43	39	36	40

Height of Hensen's cells

	TURN I	II	III	IV	AVERAGE
(N.)	20	23	23	24	23
(H.)	42	45	38	30	39

Angle of lamina basilaris with plane of membrana basilaris—degrees

	TURN I	II	III	IV	AVERAGE
(N.)	0	0	0	0	0
(H.)	+7	+4	−8	−7	—

Length of the inner and outer pillar cells

	INNER TURN I	II	III	IV	AVERAGE	
(N.)	35	39	41	40	39	
(H.)	36	39	42	45	41	
	OUTER TURN I	II	III	IV	AVERAGE	WEIGHTED AVERAGE
(N.)	26	26	29	29	28	30
(H.)	45	54	50	40	47	46

Volume of inner and outer hair cells—μ^3

	INNER: AVERAGE	OUTER: AVERAGE	WEIGHTED AVERAGE
(N.)	1798	1277	1407
(H.)	1815	1279	1428

TABLE 113—*Concluded*

Diameter of nuclei of the inner and outer hair cells

	INNER: AVERAGE	OUTER: AVERAGE	WEIGHTED AVERAGE
(N.)	8.3	8.0	8.1
(H.)	8.2	7.4	7.6

	DEITERS' CELLS: VOLUME μ^3	DIAMETER OF NUCLEI	LENGTH OF CELL BODY	PHALANGEAL PROCESS
(N.)	518	7.0	14	22
(H.)	1193	7.2	32	22

Ganglion spirale: diameters computed

	CELLS	NUCLEI
(N.)	13.6	8.5
(H.)	13.7	8.6

values are marks of maturity. These changes in size accord with the results given in chapter 1 at twelve days of age, though there are some differences between them in the absolute values.

Figures 7 and 8 illustrate the outlines of the tympanic wall of the membranous cochlea in nine-day-old rats which could not and could hear, respectively. These figures have been drawn from the corresponding sections at the beginning of the middle turn of the cochlea and are comparable with figures 3 to 6 and 9 to 12. On comparing figures 7 and 8, the more noticeable differences appear to be the following.

The membrana tectoria is a bit longer in the hearing rat. The appearance and the position of it with reference to the surface of the papilla spiralis is also different. In the not-hearing cochlea it has an infantile look.

The outer end of the main part does not yet reach the second row of the outer hair cells and connects with the Hensen's prominence by a thick thread. There are also many fine fibers to be seen between the basal surface of the membrane and the papilla. In the hearing rat the fine fibers are absent. The membrane reaches already the row of the outer hair cells and there is a strong connection between this part and the terminal ame (Schlussrahmen) of the lamina reticularis by a thick read as shown in figure 8. Thus the position of the membrane

above the papilla depends a little bit upon the increase of the length of the membrane itself, but chiefly upon other factors such as the inward shifting of the papilla. The membrana basilaris as a whole shows a small increase of breadth in the hearing rat. The zona arcuate, however, increases much in its breadth, while the zona pectinata rather decreases. This is due to the development of the pillar cells. The base of the inner and outer pillar cell spread much on the membrane. At the same time the length of the cells, especially of the outer, increases nearly twice as much as in the not-hearing rat.

Thus the foot of the outer pillar cell moves outward, as Böttcher ('69, '72) stated, while the inner corner of the inner pillar cell does not move in any way, as the habenula perforata stands at a fixed point. This results in a change in the form of the arch of Corti. The hitherto outward inclined arch tends to bend inward and between both inner and outer cells arises a space, the tunnel of Corti. The appearance of the tunnel seems to have some relation to hearing. The tunnel is always present in the cochleas of hearing rats. Sometimes the tunnel is present in the lower turns, but not in the upper turns in the not-hearing rats. We can say, therefore, that it probably appears through all the turns before the special function of the cochlea begins. In this way the zona arcuata of the membrana basilaris increases its breadth.

The next striking change is the rapid increase in the size of the Deiters' cells, Hensen's cells, and the resultant change of the form, with an inward shifting, of the papilla spiralis.

The Deiters' cells increase their height very rapidly; the length of the cell body becomes over twice that in the not-hearing rat, but the processus phalangeus changes only slightly. Hensen's cells develop also, but not so much as Deiters' cells. The papilla spiralis thus increases in height. On the other hand, the greater epithelial ridge vanishes inwards from the inner supporting cells and appears as a furrow—the sulcus spiralis internus. Through the pressure of these outward-lying cells the papilla spiralis swings inward as a whole, without really moving on the membrana basilaris. The lamina reticularis

becomes inclined inward instead of outward and subtends a slight angle with the plane of the membrana basilaris. The distance from the labium vestibulare to the inner edge of the head of the inner pillar cell becomes smaller through the inward shifting of the papilla.

In the hair cells and the cells of the ganglion spirale we see a smaller difference between the hearing and not-hearing rats. Only the diameter of the nuclei of the hair cells in the hearing rat diminishes a little, as it continues to do in the adult cochlea.

All the changes just enumerated begin at the base of the cochlea and progress to the apex. Therefore we see the high and outward ascending papilla spiralis in turn I, while in the upper turns the papilla is not yet so developed, is smaller in all the constituents, and shows in general the characters of a younger and less mature cochlea—conditions which disappear with age. This upper and immature part seems not to respond to the test for hearing. Indeed, my testing result is positive for sounds of high pitch, but not for low pitch. Therefore we conclude that the papilla spiralis develops functionally from base to apex and that when the papilla spiralis has developed in the basal turns, but not in the upper turns, it responds to sounds of high pitch alone.

Discussion

If we assume that our tests for hearing are trustworthy, then the differences between the size of the constituents of the cochlea in nine-day-old rats which could and could not hear will indicate what developmental changes in the cochlea of the albino rat are necessary for the appearance of the hearing reflex. Whether all the differences found by us are necessary is difficult to determine, and the problem is open for further study; but as the matter stands, our results give the closest correlation between structural changes and the appearance of function which has as yet been reported.

Kreidl and Yanase ('07) studied the differences between the not-hearing and hearing rat and summarized their results on page 509: "Kurz vor Eintritt des Hörreflexes ist das Cortische

Organ im wesentlichen fertig ausgebildet." They publish no measurements nor data. The condition of the development of the organ of Corti described as 'fertig ausgebildet' is not sufficiently precise.

Further, on the same page they say, "Der auffälligste und, soweit die Untersuchungen bis jetzt eregben haben, einzige Unterchied, der zwischen dem anatomischen Bild des Labyrinthes eines neugeborenen Tieres, das den Reflex eben noch nicht aufweist, und dem eines solchen, das denselben zum ersten Male eben erkennan lässt, ist der, dass beim ersteren noch ein Zusammenhang zwischen Cortischem Organ und Cortischer Membran besteht, beim letzteren dagegen dieser Zusammenhang bereits gelöst oder gelockert ist." Their observation is quite different from mine. In my case the papilla spiralis shows in the development of its constituent elements pretty large differences between the not-hearing and hearing rats. Therefore it seems probable that the changes in the growth and form of the papilla just before the first appearance of the special function, take place very quickly. Also we cannot agree to their statement concerning the relation of the membrana tectoria to the papilla spiralis. In our preparations there is still a connection of the membrane with the terminal frame of the lamina reticularis through a thick thread in the cochlea of the rat which could hear (fig. 8) and also in that of the rat which could not hear (fig. 7).

This is a point on which opinions differ. While one opinion, represented by Kishi ('07) and others, is to the effect that this connection remains through life, the other, represented by Kölliker ('67) and others, asserts the membrane projects free in the endolymph. I have never seen this connection in the adult cochlea, nor have I found such a connection of the membrane with the hairs of the hair cells, as Shambaugh ('10) described in the pig. In the young rats, at fifteen days for example, we very often see upon the terminal frame the broken remainder of this connecting thread. Whether this break arises through natural development or is the result of artificial manipulation it is hard to say. At any rate, Held's assertion ('90), that in an animal capable of hearing the membrana tectoria is never connected

with the papilla spiralis, is not supported by my observation. That the freeing of the outer zone of the membrane is not absolutely necessary for the mediation of auditory impulses is demonstrated in the cochlea of birds, as shown by Hasse ('66), Retzius ('84), Sato ('17), and others. In these forms the membrane remains through life attached to the epithelial ridge.

My results agree with those of Hardesty ('15) on this point, though he obtained a tectorial membrane which floats free in the endolymph with its outer zone. Lane ('17) studied the correlation between the structure of the papilla spiralis and the appearance of hearing in the albino rat, but his description is brief and does not touch on this relation of the papilla to the tectorial membrane.

Thus the inception of hearing does not coincide with the detachment of the tectorial membrane from the papilla spiralis, but with the development of each constituent of the papilla spiralis and the membrane tectoria, as has been described. As these changes occur first at the base and then pass to the apex, the animal can perceive at first only the sounds of high pitch. One or two days later development is complete in all the turns, and then the rat can hear the sounds of lower pitch also. Thus the process of the development of the cochlea does not support the 'telephone theory' of audition, but on the contrary agrees with the conclusion that the papilla in different locations in the turns of the cochlea responds to sounds of a definite pitch, as Wittmaack ('07), Yoshii ('09), Hoessli ('12), and others have shown by experimental studies on the mammals.

Concerning the exact age of the first appearance of the function in the rat, there are several different statements. Lane ('17) found no response to sound before the twelfth day after birth, and on the sixteenth day he reports hearing well established. Kreidl and Yanase ('07) state that hearing begins in the rat at from twelve to fourteen days. My rats responded usually at ten to twelve days, but one at nine days. These differences depend in all probability on the vigor of the young during the first days of postnatal life, and it seems probable that exceptionally well-nourished young might develop precociously in this

respect. The intensity of the stimulus is important in determining the hearing reflex, as Small ('99) has stated. In my cases the young rats responded very evidently to intense sounds, while they reacted weakly or not at all to those which were faint. Thus only the intense sounds were perceived by the rat of nine days.

Conclusions

1. The hearing reflex was never obtained in rats less than nine days of age.

2. At nine days a single rat, one of five in a litter, responded to a sharp sound like clapping the hands and to a whistle of high pitch; the other four did not respond. At the tenth day some of the four reacted, and at the twelfth day all could hear.

3. The hearing reflex probably occurs early in young rats that are vigorous and well nourished.

4. To obtain the first hearing reflexes it is necessary to have rather strong sounds of high pitch.

5. A comparison of the histological structure of the cochlea in rats of nine days, one of which could hear and the other could not, shows clear differences in its development of the cochlea. These consist not in the detachment of the tectorial membrane from the papilla spiralis, but in the degree of differentiation of the constituents of the papilla. The tectorial membrane is connected in both cases at its outer end with the terminal frame of the lamina reticularis by a thick thread. The papilla is more differentiated in the hearing rat in several characters. The tectorial membrane has reached with its outer end the outermost row of the outer hair cells, but in the not-hearing rat it has not yet reached the second row of the cells.

6. The form of the papilla and its relation to the surrounding structures, especially to the tectorial membrane, are in the hearing rat at nine days very similar to those in the rat at twelve days of age, though there are some differences between them in absolute size.

7. The freeing of the tectorial membrane from the papilla spiralis is not necessary to the appearance of the hearing reflex,

but the differentiation of the papilla, its shifting inward, its change in form and position under the membrana tectoria, appear to be important.

8. Since the papilla develops from the base toward the apex, it first reaches in the lower turn a high degree of differentiation, and this part first begins to function. Therefore the rat can hear only sounds of high pitch when it first responds.

9. This result accords with that well-known fact that the papilla in the lower turn responds to sounds of a high pitch, while in the upper turn it responds to sounds of low pitch.

III. ON THE GROWTH OF THE LARGEST NERVE CELLS IN THE GANGLION VESTIBULARE

Material and technique

The material used for the present study was in a great part the same that was employed for the studies reported in chapter 1, with the addition of some new specimens as shown in table 114 and table 94. In the slides obtained in the radial vertical section we see the vestibular ganglion cells situated in a single group at the radix of the cochlea (Fig. 3 G. V.). As four ears were used in each age group, four cell groups were examined at each age. Besides these fourteen age groups, six rats used for cross-sections, in chapter 1, were also included.

The measurements were made in the same way and under the same conditions as those described earlier for the cells of the spiral ganglion. Since the ganglion vestibulare consists of two parts, the ganglion vestibulare superius and inferius, the ten largest cells were taken from each part and the results averaged.

Observations

By way of introduction I wish to say a word about equilibration in the young rat. The young just born crawl over on each other and seem to attempt to find the mothers nipples. They turn the head to and fro and roll over on the flanks, belly, or back. While resting they take their normal position or lie on the side. When turned on their backs they endeavor to regain the normal

position. The fore legs are of more use than the hind in making readjustments. The tails hang down between the hind legs.

TABLE 114

Data on rats used for the study of the cells of the ganglion vestibulare (radial section). See also table 94

AGE	BODY WEIGHT	BODY LENGTH	SEX	SIDE	AUDITORY RESPONSE
days	*grams*	*mm.*			
1	5	44	♀	R.	—
	4	44	♀	R.	—
	5	48	♂	R. L.	—
3	9	60	♂	R. L.	—
	8	56	♀	R. L.	—
6	10	64	♂	R.	—
	10	64	♀	R. L.	—
	11	62	♂	R.	—
9	11	67	♂	R. L.	+
	9	58	♀	R.	—
	10	57	♂	R.	±
12	13	70	♂	R. L.	+
	12	68	♀	R.	+
	15	72	♂	R.	+
15	13	74	♂	R. L.	+
	14	75	♀	R. L.	+
20	30	96	♂	R. L.	+
	28	94	♂	R. L.	+
25	34	101	♀	R. L.	+
	34	100	♂	R. L.	+
50	58	121	♀	R. L.	+
	43	104	♂	R. L.	+
100	146	176	♂	L.	+
	103	154	♀	L.	+
	101	152	♀	R. L.	+
150	154	184	♀	R. L.	+
	189	191	♂	R.	+
	199	192	♂	R.	+
260	137	162	♀	R.	+
	140	171	♀	R. L.	+
	134	178	♀	R.	+
367	205	202	♂	L.	+
	170	182	♀	L.	+
	179	196	♀	R. L.	+
546	282	222	♂	R. L.	+
	227	204	♂	R. L.	+

At three days they move and crawl very actively. They tend to assume the normal position. When rolled over on the back or side they succeed in regaining the normal position in

a few seconds. When six days old the rats have fairly well coordinated movements. They use their fore and hind legs effectively and in the same way. When the mother's body touches them they respond quickly by searching for the nipples.

At nine days they move much more quickly and the movements are well coordinated. Though the eyes are still closed, they

TABLE 115

Diameters of the cells and their nuclei in the ganglion vestibulare in radial vertical section (Chart 43)

AGE	BODY WEIGHT	DIAMETERS IN μ					
		CELL BODY			NUCLEUS		
		Long	Short	Computed	Long	Short	Computed
days	*grams*						
1	5	21.2	19.5	20.3	12.4	11.1	11.7
3	9	23.7	22.2	22.9	12.5	11.6	12.0
6	11	24.0	22.1	23.0	12.3	11.9	11.9
9	10	24.8	23.0	23.9	12.5	11.6	12.0
12	13	24.9	23.0	23.9	12.5	11.7	12.1
15	13	24.8	23.0	23.9	12.5	11.6	12.0
20	27	25.0	23.3	24.1	12.3	11.6	11.9
25	34	25.2	23.6	24.4	12.5	11.8	12.1
50	50	25.6	23.6	24.5	12.5	11.6	12.0
100	112	25.5	23.9	24.7	12.8	11.9	12.3
150	174	25.4	23.5	24.4	12.8	11.6	12.2
260	138	25.8	23.4	24.6	12.4	11.7	12.0
367	184	26.2	24.9	25.5	12.9	11.8	12.3
546	255	26.5	24.2	25.3	12.8	11.8	12.2
Ratios 1—367 days				1 : 1.3			1:1.1
1—546 "				: 1.2			:1.0
15—367 "				: 1.1			:1.0

crawl toward the object sought. When turned over on the back they regain the normal position immediately. While resting they lie on their bellies with all the legs spread well apart.

Twelve-day-old rats, though the eyes are still closed, go to and fro actively with good coordination, but are somewhat slower than the adults. The body loses its fetal red color through the development of the first hairs. After this period the rats do not differ greatly from the adult in their general behavior.

The growth changes in the ganglion cells of the ganglion vestibulare. In table 115 (chart 43) are given the values for the diameters of the cell bodies and their nuclei in the largest cells of the ganglion vestibulare. At the bottom of the last column for the cell body and for the nucleus, respectively, are recorded the ratios at 1 to 367; 1 to 546, and 15 to 367 days. The last ratio was taken

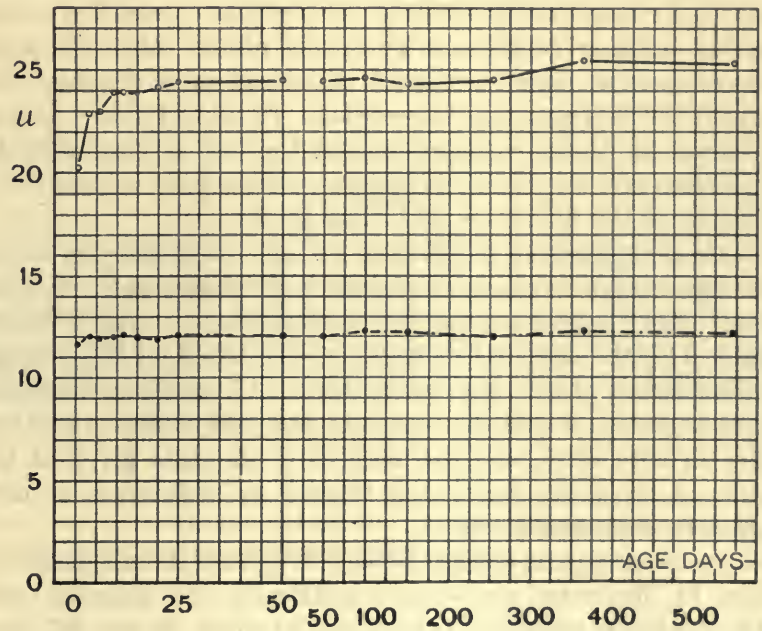

Chart 43 The diameter of the largest cell bodies and of the nuclei from the ganglion vestibulare, table 115.
———— Cell bodies. –.–.–.–.–. Nuclei.

to facilitate a comparison with the data in table 118 which begin at 15 days.

Looking at the ratios of the cell bodies and of their nuclei from 1 to 546 days, it appears that the ganglion cells increase 1.2 in diameter, while their nuclei have only a very slight increase, and therefore the ratio is 1: 1.0. This increase in the cell bodies is continuous from birth to old age, but after fifteen days is very slow. In the nucleus we see a slight increase at the earlier

ages, after which the values are nearly constant. This means that after birth the size of the cell bodies and their nuclei does not increase so much as do those of the spiral ganglion cells, or, expressed in another way, the cells in the vestibular ganglion have developed earlier than those of the spiral ganglia and at birth have already attained nearly their full size.

On the comparison of the diameter of the cell bodies and their nuclei in the nerve cells of the ganglion vestibulare according to sex. For this purpose twelve age groups of albino rats were used. In seven cases we have two cochlea in each group in the same sex, in which the average value is recorded. In table 116 are entered the values for these diameters and at the foot of the table the data are analysed. They reveal no evidence of a significant difference in the diameters according to sex.

On the comparison of the diameters in the cell bodies and nuclei of the nerve cells in the ganglion vestibulare according to side. For the present study fourteen age groups were employed. As indicated in table 117, the data in five instances are based on the average of two cochleas of the same side. Table 117 enables us to make the comparison of the diameters of the cell bodies and their nuclei on both sides, and the analysis of the data given at the bottom of the table shows that there is no difference in these characters according to side.

On the morphological changes in the cells of the vestibular ganglion. Figure 14 illustrates semi-diagrammatically the ganglion cells in the vestibular ganglion of the albino at birth, 20 and 367 days of age. These figures, as in the ganglion spirale, have been magnified 1000 times and the absolute values of the diameters are given in table 115.

As seen in figure 14, both the cell body and the nucleus are at birth already well developed and more precocious in their development than the cells in any of the other cerebrospinal ganglia thus far examined. The cytoplasm is relatively abundant and the Nissl bodies are present, though both of these characters become more marked later.

The nucleus is also large, the chromatin somewhat differentiated and the so-called 'Kernfaden' often occur. Generally speaking,

Fig. 14 Showing semi-diagrammatically the size and the morphological changes in the ganglion cells in the ganglion vestibulare of the albino rat at the age of 1, 20 and 366 days. All cell figures have been magnified 1000 diameters.

therefore, the cells have the characteristics of the mature elements though they stain less deeply than in the adult. At twenty days of age the cell body is enlarged and fully mature. The Nissl

TABLE 116

Comparison of the diameters of the cells and their nuclei in the ganglion vestibulare —accerding to sex

AGE	BODY WEIGHT	NUMBER OF RATS	SEX	COMPUTED DIAMETERS	
				Cell body	Nucleus
days	*grams*				
1	5	2	♂	20.8	11.9
			♀	19.9	11.5
3	9	2	♂	21.7	11.8
	8	2	♀	23.8	12.2
6	11	2	♂	22.7	11.9
	10	2	♀	23.1	12.1
9	11	1	♂	23.8	12.5
	9	1	♀	23.8	12.1
12	15	1	♂	24.4	12.2
	12	1	♀	23.1	11.9
15	13	2	♂	24.3	12.2
	13	2	♀	23.4	11.9
20	30	1	♂	24.7	11.9
	19	1	♀	24.6	12.6
25	34	2	♂	24.4	11.9
	34	2	♀	24.4	12.4
50	43	2	♂	26.1	12.4
	58	2	♀	22.6	11.4
100	146	1	♂	26.3	12.8
	103	1	♀	23.4	12.6
150	194	2	♂	24.4	12.5
	154	2	♀	24.4	12.0
365	205	1	♂	24.2	11.7
	170	1	♀	24.6	12.1
Average for male				24.0	12.1
Average for female				23.4	12.1
Males larger				6	7
Females larger				3	5
Males and females equal				3	0

bodies are more differentiated and the nucleus is mature, though it shows only a slight increase in size.

At 367 days the histological structures appear much as at twenty days, but the diameters of both the cell body and the nucleus have very slightly increased. This is in contrast to the change which occurs in the cells of the spiral ganglion.

In order to study the form of the cells of the ganglion vestibulare the measurements also were made on the cross-sections. Table

TABLE 117

Comparison of the diameters of the cells and their nuclei in the ganglion vestibulare—according to side

AGE	BODY WEIGHT	NUMBER OF RATS	SIDE	COMPUTED DIAMETERS	
				Cell body	Nucleus
days	*grams*				
1	4	1	R.	20.1	12.0
	5	1	L.	22.0	12.5
3	9	2	R.	23.0	11.8
			L.	22.6	12.3
6	10	1	R.	23.2	12.1
			L.	23.5	12.0
9	11	1	R.	25.1	12.3
			L.	23.8	12.5
12	15	1	R.	24.4	12.2
	13	1	L.	25.1	12.5
15	13	2	R.	24.2	12.2
			L.	23.6	11.9
20	30	1	R.	24.7	11.9
			L.	23.5	11.4
25	34	2	R.	23.9	12.1
			L.	24.9	12.2
50	50	2	R.	23.1	11.6
			L.	25.6	12.3
100	101	1	R.	25.0	12.0
			L.	24.8	11.7
150	199	1	R.	25.1	12.8
	154	1	L.	25.4	12.5
263	140	1	R.	26.5	12.3
			L.	25.1	12.4
368	179	1	R.	27.2	12.6
			L.	26.2	13.0
546	255	2	R.	26.0	12.4
			L.	24.6	12.0
		Average right side		24.4	12.2
		Average left side		24.3	12.2
		Right larger		8	6
		Left larger		6	8

118 (chart 44) shows the results. Looking at the ratios of 15 to 371 days, we see the same rate of increase in the cell bodies and the nuclei as that in the radial section; i.e., in the cell bodies 1: 1.1 and in the nuclei 1: 1.0. Comparing the diameters at each

TABLE 118

Diameters of the cell bodies and their nuclei in the ganglion vestibulare, on cross-section (chart 44)

AGE	BODY WEIGHT	DIAMETERS— μ					
		CELL BODY			NUCLEUS		
		Long	Short	Computed	Long	Short	Computed
days	*grams*						
15	20	25.1	22.8	23.9	12.4	11.6	12.0
20	27	25.2	23.4	24.3	12.5	11.7	12.1
25	39	25.2	24.0	24.6	12.3	12.0	12.1
100	95	26.6	24.7	25.6	12.8	11.8	12.3
150	169	26.7	24.7	25.7	13.0	11.7	12.3
371	220	26.8	25.3	26.0	12.8	11.8	12.3
Ratio 15–371 days				1 : 1.1			1 : 1.0

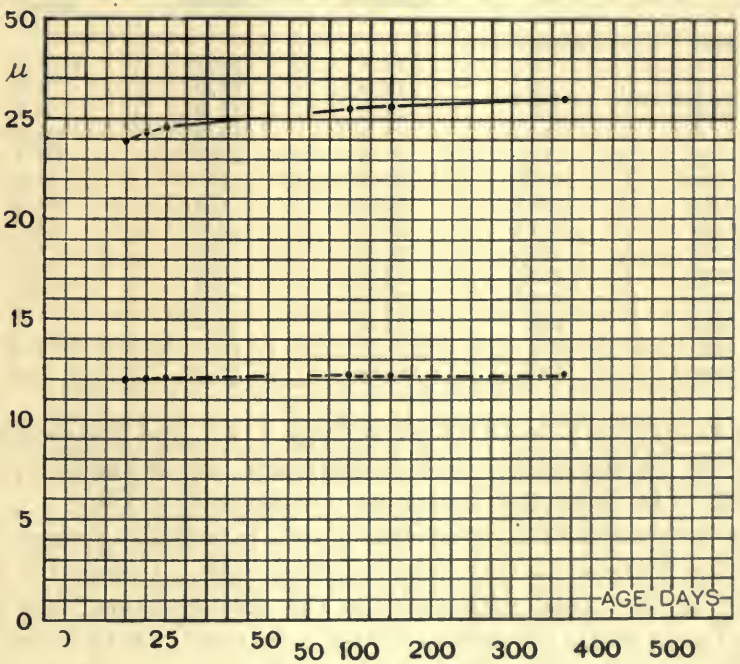

Chart 44 The diameters of the cell bodies and of their nuclei from the ganglion vestibulare, after fifteen days (cross-section), table 118.

———— Cell bodies. –.–.–.–.–. Nuclei.

age in both the radial and cross-sections, they are almost the same, with a slight tendency for the cells in the cross-section to give higher values, which suggests that the long axes of these cells tend to lie in the plane of the section.

On the nucleus-plasma relations of the ganglion cells in the ganlion vestibulare. In table 119 are entered the computed diameters of the cell bodies and their nuclei in the radial section, and in the last column the ratios of the volume of the nucleus to that of the cytoplasm obtained by the method previously given. As

TABLE 119

Nucleus-plasma ratios of the cells in the ganglion vestibulare—radial vertical section

AGE	BODY WEIGHT	COMPUTED DIAMETERS— μ		
		Cell body	Nucleus	Nucleus-plasma ratios
days	*grams*			
1	5	20.3	11.7	1 : 4.2
3	9	22.9	12.0	: 5.9
6	11	23.0	11.9	: 6.2
9	10	23.9	12.0	: 6.9
12	13	23.9	12.1	: 6.7
15	13	23.9	12.0	: 6.9
20	27	24.1	11.9	: 7.3
25	34	24.4	12.1	: 7.2
50	50	24.5	12.0	: 7.5
100	112	24.7	12.3	: 7.1
150	174	24.4	12.2	: 7.0
260	138	24.6	12.0	: 7.6
367	184	25.5	12.3	: 7.9
546	255	25.3	12.2	: 7.9

seen, the ratio is at birth relatively large, 1 : 4.2, and this increases with age, in the earlier stages considerably, but in the later, less rapidly. In the oldest age group it is largest, 1 : 7.9.

On the cross-section the nucleus-plasma ratio is also progressive and the increase is very regular (table 120). Comparing the ratios in the radial with those in the cross-sections, they are found to be nearly the same at fifteen twenty and twenty-five days, but at the later ages those in the cross-sections are somewhat larger than in the radial. It is difficult to determine whether the ratios on the cross-section are really larger or whether the

result depends on the fact that the number of the cells here measured is only one-fourth of that measured in the radial section, and hence fewer cells of smaller size were included. At any rate, these ganglion cells in both the radial and cross-sections of the cochlea appear to grow at about the same rate.

The statistical constants for these cells and their nuclei are given in tables 121 and 122.

Discussion

The nerve cells in the ganglion vestibulare are, as seen from the above description, already well developed at birth both in size and histological structure. After that time they grow con-

TABLE 120

Nucleus-plasma ratios of cells of the ganglion vestibulare, in cross-section

AGE	BODY WEIGHT	DIAMETERS COMPUTED μ		
		Cell body	Nucleus	Nucleus-plasma ratios
days	*grams*			
15	20	23.9	12.0	1 : 6.9
20	27	24.3	12.1	: 7.1
25	39	24.6	12.1	: 7.4
100	95	25.6	12.3	: 8.0
150	169	25.7	12.3	: 8.1
371	220	26.0	12.3	: 8.4

tinuously but slowly so long as followed. The increase from 1 to 546 days in the ratios of the diameters is in the cell body 1: 1.3, in the nucleus 1: 1.1, and is therefore very small. In the cerebrospinal ganglion cells and in the cells of the cerebral cortex, studied in the albino rat, there is no case which shows such a small rate of increase between birth and maturity. The following table 123 shows the ratios of increase which have been found.

It is to be noted that for the cells of the seventh spinal ganglion and the spinal cord, the ratios were taken from 17 to 360 days. If we had the ratios from 1 to 360 days, they would be without question much larger.

There are a few measurements on the size of the ganglion cells in the vestibular ganglion of various animals in the liter-

ature. Schwalbe ('87) and Alexander ('99) report measurements on these cells in several animals, but for the reasons already given when considering the diameters of the cells in the ganglion spirale, the values obtained by the authors are not repeated here.

TABLE 121

Giving the mean, standard deviation and coefficient of variability, with their respective probable errors, for the diameters of the cells in the ganglion vestibulare, in radial-vertical section

AGE	CELL NUCLEUS	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
days				
1	Cell	20.1 ± 0.16	1.46 ± 0.11	7.3 ± 0.55
	Nucleus	11.7 ± 0.11	0.99 ± 0.07	8.5 ± 0.64
3	Cell	22.6 ± 0.14	1.33 ± 0.10	5.9 ± 0.44
	Nucleus	11.9 ± 0.07	0.63 ± 0.05	5.3 ± 0.40
6	Cell	22.8 ± 0.13	1.23 ± 0.09	5.4 ± 0.41
	Nucleus	11.9 ± 0.05	0.43 ± 0.03	3.6 ± 0.27
9	Cell	23.6 ± 0.16	1.48 ± 0.11	6.3 ± 0.48
	Nucleus	12.0 ± 0.09	0.82 ± 0.06	6.8 ± 0.52
12	Cell	23.6 ± 0.14	1.28 ± 0.10	5.4 ± 0.41
	Nucleus	12.0 ± 0.06	0.59 ± 0.04	4.9 ± 0.37
15	Cell	23.6 ± 0.13	1.21 ± 0.09	5.1 ± 0.39
	Nucleus	12.1 ± 0.06	0.60 ± 0.05	5.0 ± 0.38
20	Cell	23.9 ± 0.16	1.54 ± 0.11	6.5 ± 0.49
	Nucleus	11.9 ± 0.10	0.90 ± 0.07	7.6 ± 0.55
25	Cell	24.2 ± 0.16	1.48 ± 0.11	6.1 ± 0.46
	Nucleus	12.1 ± 0.08	0.74 ± 0.06	6.1 ± 0.46
50	Cell	24.1 ± 0.30	2.80 ± 0.21	11.6 ± 0.88
	Nucleus	11.8 ± 0.09	0.86 ± 0.06	7.3 ± 0.55
100	Cell	24.3 ± 0.20	1.86 ± 0.14	7.7 ± 0.58
	Nucleus	12.2 ± 0.09	0.86 ± 0.06	7.0 ± 0.53
150	Cell	24.1 ± 0.18	1.70 ± 0.13	7.1 ± 0.53
	Nucleus	12.2 ± 0.09	0.83 ± 0.06	6.8 ± 0.52
260	Cell	24.3 ± 0.26	2.45 ± 0.18	10.1 ± 0.76
	Nucleus	11.9 ± 0.07	0.67 ± 0.05	5.6 ± 0.42
367	Cell	25.2 ± 0.22	2.07 ± 0.16	8.2 ± 0.62
	Nucleus	12.3 ± 0.09	0.88 ± 0.07	7.2 ± 0.54
546	Cell	25.0 ± 0.19	1.80 ± 0.14	7.2 ± 0.54
	Nucleus	12.1 ± 0.09	0.81 ± 0.06	6.7 ± 0.50

On the differences between the growth of the cells in the ganglion spirale and ganglion vestibulare. The foregoing discussion has made plain that the vestibular ganglion cells grow not only in size, but also in histological structure very much before birth, while after birth they grow slowly though continuously. On the other hand, the spiral ganglion cells are relatively immature at

birth, but in the earlier stages after birth grow very rapidly, reach at twenty days their maximum size, and then diminish slowly. This great difference in the course of growth is probably related to the maturity of the functions of the animal.

TABLE 122

Giving the mean, standard deviation and coefficient of variability with their respective probable errors for the diameters of the cells in the ganglion vestibulare on cross-section

AGE *days*	CELL NUCLEUS	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
15	Cell	23.8 ± 0.21	1.00 ± 0.15	4.2 ± 0.58
	Nucleus	12.0 ± 0.12	0.55 ± 0.08	4.6 ± 0.69
20	Cell	23.9 ± 0.20	0.92 ± 0.14	3.9 ± 0.58
	Nucleus	12.1 ± 0.06	0.30 ± 0.05	2.5 ± 0.37
25	Cell	24.4 ± 0.20	0.94 ± 0.14	3.9 ± 0.58
	Nucleus	12.1 ± 0.03	0.16 ± 0.02	1.3 ± 0.20
100	Cell	25.4 ± 0.32	1.51 ± 0.23	5.9 ± 0.90
	Nucleus	12.3 ± 0.15	0.72 ± 0.11	5.9 ± 0.88
150	Cell	25.6 ± 0.20	0.94 ± 0.14	3.7 ± 0.55
	Nucleus	12.4 ± 0.09	0.42 ± 0.06	3.4 ± 0.51
371	Cell	25.9 ± 0.41	1.91 ± 0.29	7.4 ± 1.11
	Nucleus	12.3 ± 0.06	0.26 ± 0.04	2.1 ± 0.32

TABLE 123

Ratios of diameters between the ages given.

CELL GROUP	CEREBRAL CORTEX (SUGITA, '18)					DONALDSON AND NAGASAKA, '18	
	LAMINA PYRAMIDIS	LAMINA GANGLIONARIS	GASSERIAN GANGLION NITTONO ('20)	SPIRAL GANGLION WADA	VESTIBULAR GANGLION WADA	7TH SPINAL GANGLION	EFFERENT SPINAL CORD CELLS
Age—days	1–730	1–730	1–330	1–546	1–546	17–360	17–360
Cell body	1 : 1.6	1 : 1.6	1 : 1.69	1 : 1.6	1 : 1.2	1 : 1.3	1 : 1.2
Nucleus	: 1.5	: 1.5	: 1.20	: 1.2	: 1.0	: 1.2	: 1.2

As a consequence, in the nucleus-plasma ratio there is also a large difference between the cells in the two ganglia. Table 124 shows this.

The ratio at birth in the ganglion vestibulare is large as compared with that in the ganglion spirale, but the increase in this ratio

at 546 days is relatively slight as compared with what takes place in the cells of the ganglion spirale. It appears, therefore, that the cells in the vestibular ganglion are at birth in a more mature condition.

As to the correlation between the development of the ganglion cells and the equilibrium function, we have noted that the albino rats, even just after birth, show some sense of equilibrium, though the movements are lacking in coordination. With advancing age the balance of the body is held much better and all the movements gradually become coordinated. The histological structure and the size of the cells at birth suggest that they are functional at that time, and the later increase in the volume and maturity of the cells is accompanied by a corresponding

TABLE 124

	GANGLION VESTIBULARE	GANGLION SPIRALE
Nucleus-plasma ratio at one day	1 : 4.8	1 : 1.3
Nucleus-plasma ratio at 546 days	: 7.9	: 4.2

increase in the functional development. When the tactile sense is well developed and the eyes open equilibrium is almost perfected.

It is a well-known fact that these two senses have very intimate relations to the maintenance of equilibrium. In this case, as we might expect, the early development of a function is accompanied by an early maturing of the neural mechanism on which it depends.

Conclusions (for the ganglion vestibulare)

1. The measurements were taken on the largest nerve cells of the ganglion vestibulare in the radial section of the cochlea, and the developmental changes during portnatal growth studied in fourteen age groups, comprising four ears in each group. Further, in six age groups the cell size was determined in cross-sections. The results have been given in tables 115 and 118 and charts 43 and 44.

2. The computed diameter at birth is 20.3 μ for the cell body and 11.7 μ for the nucleus, and at 546 days, 25.3 and 12.2 μ, respectively. Therefore the cells at birth are comparatively large and increase in size very slowly, but the increase is continuous.

3. The increase in the ratio of the cell body is as 1: 1.3, of the nucleus as 1: 1.1. We have between the same age limits no such small rate of increase in any other cerebrospinal ganglion studied in the albino rat. This small ratio indicates that the cells in the vestibular ganglion are well developed at birth.

4. We find no appreciable difference in the diameters of the cell bodies or the nuclei according either to sex or side.

5. Morphologically, the cells at birth are well differentiated. The form of the cells is ovoid.

6. The nucleus-plasma ratios are large at birth and increase regularly with age.

7. Comparing the development of the function of equilibrium with the growth of the cells, we see that these are correlated.

Final summary

This study is concerned with the age changes in the organ of Corti and the associated structures. The changes in the largest nerve cells which constitute the spiral ganglion and the vestibular ganglion, respectively, have also been followed from birth to maturity. On pages 116 to 124 are given the summary and discussion of the observations on the growth of the tympanic wall of the ductus cochlearis.

The conclusions reached from the study of the largest nerve cells in the ganglion spirale appear on pages 143 to 145. On pages 155 and 156 are presented the results of the study on the correlation between the response to sound and to the conditions of the cochlea.

Finally, the observations on the growth of the largest cells in the ganglion vestibu'are are summarized on pages 168 and 169.

It is not necessary to again state in detail the conclusions reached in the various parts of this study.

At the same time, if we endeavor to obtain a very general picture of the events and changes thus described, this may be sketched as follows:

Within the membranous cochlea there occurs a wave of growth passing from the axis to the periphery as shown in figures 4 to 13. The crest or highest point of the tissue mass appears at birth near the axis, in the greater epithelial ridge, and then progressively shifts toward the periphery, so that at maturity it is in the region of the Hensen cells. With advancing age the hair cells come to lie more and more under the tectorial membrane and the pillar cells seem to shift toward the axis.

At from 9 to 12 days the tunnel of Corti appears and the rat can hear.

All of these changes occur first in the basal turn and progress toward the apex. The mature relations are established at about twenty days. There are thus two waves of change in the membranous cochlea, from the axis to the periphery and the other from the base to the apex. The rat can usually hear at twelve days of age or about three days before the eyes open.

The largest cells in the ganglion spirale are very immature at birth, reach their maximum at twenty days, and after that diminish in size, slightly but steadily. The rat hears, therefore, before these cells have reached their full size.

The largest cells in the vestibular ganglion are precocious and remarkably developed, even at birth. They cease their rapid growth at about fifteen days of age, but increase very slightly though steadily throughout life.

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